UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ÉTUDE DES FACTEURS ENVIRONNEMENTAUX STRUCTURANT LA DIVERSITÉ ET LA DISTRIBUTION DES COMMUNAUTÉS BENTHIQUES DE L'ARCTIQUE CANADIEN

STUDYING ENVIRONMENTAL FACTORS STRUCTURING BENTHIC DIVERSITY AND COMMUNITY DISTRIBUTION IN THE CANADIAN ARCTIC

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« *La connaissance est une navigation dans un océan d'incertitudes*
à travers des archipels de certitudes. »
Edgar Morin

« *Quand nous avons soif, il nous semble que nous pourrions boire*
tout un océan : c'est la foi. Et quand nous nous mettons à
boire, nous buvons un verre ou deux : c'est la science. »
Anton Tchekhov

« *Quiconque prétend s'ériger en juge de la vérité et du savoir*
s'expose à périr sous les éclats de rire des dieux puisque nous
ignorons comment sont réellement les choses et que nous n'en
connaissons que la représentation que nous en faisons. »
Albert Einstein

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Les écosystèmes aquatiques m'ont toujours passionnée, et c'est avec passion et curiosité que j'ai plongé dans ce projet en océanographie-biologie. L'ensemble de ma thèse reflète bien mon désir personnel et constant de vouloir comprendre au maximum une problématique. Les deux premières années de ma thèse ont été chaotiques, car l'idée de départ pour mon projet de doctorat était d'étudier l'importance de l'hétérogénéité topographique pour les communautés benthiques à l'échelle de l'Arctique canadien. Or, ce projet s'est avéré difficilement réalisable dans le contexte actuel de disponibilité de données, du plan d'échantillonnage et d'avancement de la technologie dans l'Arctique canadien. Je reviens brièvement sur cette idée de recherche dans les perspectives de recherche à la fin de la thèse. J'ai dû réorienter ma thèse rapidement, une réorientation certes difficile, mais dont je suis maintenant satisfaite. Elle a donné lieu à quatre chapitres, brièvement introduits ci-dessous.

Dans le contexte des deux premiers chapitres, je me suis intéressée particulièrement à la classe de taille de la mégafaune benthique, puisqu'à ce jour aucune étude dans l'Arctique canadien et peu d'études ailleurs en Arctique ont été consacrées à l'étude de la variabilité de la diversité et de la distribution de ces communautés. Par conséquent, cette thèse apporte pour la première fois à l'échelle de l'Arctique canadien des données de référence sur la richesse et la composition taxonomique de la mégafaune benthique (chapitre 1) et détermine les facteurs environnementaux structurant les patrons de distribution de ces communautés (chapitre 2). Le premier chapitre de cette thèse fera l'objet d'un article qui a été soumis à la revue *Arctic*, alors que le deuxième chapitre a fait l'objet d'un article publié dans la revue *PLoS ONE*.

Pour le chapitre 3, je tenais à générer des modèles prédictifs pour la région de la mer de Beaufort et le golfe d'Amundsen, des régions d'intérêt grandissant pour l'exploitation de sources d'hydrocarbures. Ces modèles sont non seulement utiles pour accroître notre compréhension du contrôle environnemental sur les communautés benthiques, mais également pour permettre l'amélioration des processus gouvernementaux de conservation, notamment la désignation de zones d'importance écologique et biologique (ZIEB). Ce chapitre a été rendu possible grâce à l'assemblage de plusieurs bases de données sur la macrofaune benthique récoltée dans le cadre de nombreux programmes scientifiques entre 1973 et 2012. Je tiens donc à exprimer ma profonde reconnaissance à tous ceux qui ont partagé leurs données. Ce chapitre fera l'objet d'un article qui a été soumis à la revue *Journal of Marine Systems*.

Pour affiner ma compréhension du contrôle environnemental sur la distribution des communautés benthiques, j'ai étudié les réponses du réseau trophique benthique en fonction de deux des plus notables gradients environnementaux qui traversent l'Arctique canadien, soit la profondeur et la production biologique (chapitre 4). En étudiant la variabilité spatiale du ratio isotopique du carbone et de l'azote de sources potentielles de nourriture pour les invertébrés benthiques, de même que les ratios isotopiques de ces derniers, ce quatrième chapitre vient clore ma thèse en mettant en lumière certains des processus expliquant les relations environnement – communautés exposées dans les trois premiers chapitres. Ce chapitre fera l'objet d'un article qui a été soumis à la revue *Deep-Sea Research Part I.*

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Axes ou thèmes de recherche dans lesquels fait partie ce projet :

- **ArcticNet** : Phase 3 (2011-2014) - Impacts des changements climatiques sur l'écosystème benthique arctique
- **CHONe** : Thème 1 - Biodiversité Marine
- **Québec-Océan** : Axe 4 - Fonctionnement et intégrité des écosystèmes marins arctiques et subarctiques
- **Laboratoire d'écologie benthique de l'ISMER** : cette thèse s'inscrit dans un projet à long terme qui tente d'établir un cadre de référence de la diversité et de la distribution de la faune benthique dans l'Arctique canadien afin de suivre l'intégrité des écosystèmes marins benthiques dans les années à venir.

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Liste des publications issues de la thèse

Roy V., Iken K., Archambault P. (chapitre 1) Regional variability of megabenthic community structure across the Canadian Arctic. Soumis pour publication dans la revue *Arctic*.

Roy V., Iken K., Archambault P. (chapitre 2) 2014. Environmental drivers of the Canadian Arctic megabenthic communities. *PLoS ONE*, 9(7): e100900.

Roy V., Archambault P., Conlan K., Hendrycks E., Aitken A. (chapitre 3) Predictive models of macrobenthos patterns in the southeastern Beaufort Sea and Amundsen Gulf. Soumis pour publication dans la revue *Journal of Marine Systems*.

Roy V., Iken K., Gosselin M., Tremblay J.-É., Bélanger S., Archambault P. (chapitre 4) Benthic food-web responses to marine biological productivity and depth across the Canadian Arctic. Soumis pour publication dans la revue *Deep-Sea Research Part I*.

Cobb D.G., Roy V., Link H., Archambault P. 2014. Information to support the re-assessment of original ecologically and biologically significant areas (EBSAs) in the Beaufort Sea Large Ocean Management Area. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/nnn. Sous presse.

Roy V., Iken K., Archambault P. 2013. Canadian contribution to Arctic megabenthic diversity monitoring. e-CBMP Newsletter (Circumpolar Biodiversity Monitoring Program), Fall, 7 (2).

Roy V., Link H., Archambault P. 2012. Identification of Macro- and Megabenthic Ecologically and Biologically Significant Areas (EBSAs) in the Beaufort Sea Large Ocean Management Area (LOMA). A Working Paper on benthic systems for the CSAS meeting Nov. 20-22, 2012 in Winnipeg (MB), Canada.

Kenchington E., Link H., Roy V., Archambault P., Siferd T., Treble M., Wareham V. 2011. Identification of Mega- and Macrobenthic Ecologically and Biologically Significant Areas (EBSAs) in the Hudson Bay Complex, the Western and Eastern Canadian Arctic. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/071. vi + 52 p.

Liste des mentions issues de la thèse

Prix d'excellence, présentation orale. *Assemblée générale annuelle de Québec-Océan*, Rivière-du-Loup (Canada). Novembre 2013.

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Prix d'excellence, présentation par affiche (premier prix). *Rencontre annuelle du Réseau stratégique du CRSNG pour des océans canadiens en santé (CHONe)*, Ottawa (Canada). Octobre 2012.

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RÉSUMÉ

L'océan Arctique subit déjà et à un rythme accéléré les effets du réchauffement climatique global. La baisse constante de la couverture de glace multiannuelle et l'allongement de la période d'eau libre en été alimentent des intérêts économiques croissants dans l'Arctique canadien en raison de l'ouverture du passage du Nord-Ouest à la navigation et du potentiel d'exploitation d'hydrocarbures. Les impacts éventuels des changements climatiques et des activités anthropiques sur l'écosystème marin benthique peuvent être sévères, mais sont difficiles à évaluer et à prévoir, car peu de données de référence documentant les conditions actuelles de cet écosystème existent. L'objectif principal de cette thèse est ainsi de décrire la diversité et la distribution des communautés benthiques de l'Arctique canadien et de comprendre comment les facteurs environnementaux les structurent. Le premier recensement à ce jour de la diversité des communautés de la mégafaune benthique à l'échelle de l'Arctique canadien (chapitre 1) a permis d'étudier les facteurs environnementaux les structurant (chapitre 2). Ensuite, une étude à l'échelle régionale a permis de créer des modèles prédictifs des patrons de distribution des communautés de la macrofaune (chapitre 3). Finalement, la variabilité spatiale de réponses fonctionnelles du réseau trophique benthique le long de gradients environnementaux (chapitre 4) a été examinée afin de mieux comprendre les processus générant les relations environnement – communautés observées dans les premiers chapitres.

Tout d'abord, le chapitre 1 montre qu'au total 527 taxa de la mégafaune ont été dénombrés sur un ensemble de 78 stations à travers l'Arctique canadien. Les richesses taxonomiques moyennes observées dans cinq régions de l'Arctique canadien sont dans l'ensemble similaires, mais environ 34 % à 59 % des taxa restent à être documentés dans chacune des régions. Malgré une grande hétérogénéité d'habitats (diversité *bêta*), la région du golfe d'Amundsen présente une plus faible richesse taxonomique que dans la région voisine de la mer de Beaufort. Les communautés benthiques sont également similaires entre les régions, sauf dans le cas de la mer de Beaufort où la rivière Mackenzie influence de façon distincte la composition taxonomique.

Le chapitre 2 illustre qu'à l'échelle de l'Arctique canadien c'est une combinaison de variables environnementales, variant sur plusieurs échelles spatiales (continentale, régionale et locale), qui structurent les six communautés de la mégafaune benthique définies sur la base de la similarité de leur composition taxonomique. Dans l'ensemble, la biomasse, la densité et la richesse de la mégafaune diminuent avec la profondeur et augmentent avec la disponibilité des ressources. Cependant, le pouvoir explicatif de toutes les relations statistiques analysées est modéré, car des conditions biologiques et physiques locales et régionales, telle la présence de polynies ou de courants de fond, interfèrent avec les tendances à l'échelle continentale.

Le chapitre 3 étudie spécifiquement les facteurs environnementaux structurant les communautés de la macrofaune benthique de la mer de Beaufort et du golfe d'Amundsen, des régions où l'exploration et l'exploitation de sources d'hydrocarbures devraient s'intensifier dans un avenir rapproché. La faible variabilité temporelle des communautés a permis d'assembler plusieurs bases de données en provenance de divers programmes scientifiques entre 1973 et 2012 dans le but de créer des modèles prédictifs. Les patrons de richesse et de densité, de même que les communautés, sont distribués régionalement en fonction de la profondeur et de la salinité. À une échelle spatiale plus fine, sur le plateau continental (< 200 m), les communautés sont distribuées en fonction de la granulométrie du substrat.

Finalement, via l'examen de la variabilité spatiale de la composition des isotopes stables du carbone ($\delta^{13}C$), le chapitre 4 indique que la source principale de carbone des invertébrés benthiques de l'archipel arctique canadien provient des algues de glace. Ce fort couplage algues de glace – benthos est particulièrement évident dans les détroits de Barrow et d'Éclipse où se trouvent d'ailleurs les plus fortes biomasses d'algues de glace répertoriées jusqu'à maintenant dans l'Arctique canadien. La variabilité des ratios isotopiques de l'azote ($\delta^{15}N$) montre que comparativement à leurs homologues du plateau continental (< 200 m), les consommateurs primaires des stations profondes (≥ 200 m) assimilent de la matière organique dégradée et les prédateurs-charognards ont une diète principalement omnivore.

Cette thèse lègue dans l'ensemble de nombreuses données originales de référence pour l'Arctique canadien, entre autres sur la diversité de la mégafaune benthique. Cette recherche a permis également de montrer la complexité des relations environnement – communautés sur plusieurs échelles spatiales et apporte de nouvelles connaissances quant à l'importance actuelle des algues de glace comme source principale de carbone des communautés benthiques de l'Arctique canadien. Les résultats obtenus quant aux facteurs environnementaux principaux structurant la diversité et la distribution des communautés pourront servir dans les processus canadiens de désignation des zones d'importance écologique et biologique (ZIEB) et dans la planification nationale d'aires marines protégées et de stratégies de conservation. En outre, ces résultats aideront à orienter de futures études scientifiques ayant comme objectif l'approfondissement des processus et des mécanismes à l'origine des relations identifiées dans cette thèse.

Mots clés **:** Arctique canadien, benthos, macrofaune, mégafaune, diversité, écologie des communautés, facteurs environnementaux, variabilité spatiale, isotopes stables, couplage pélago-benthique.

ABSTRACT

The Arctic Ocean is already subject at an accelerated rate to the effects of global warming. The constant decrease of multiannual ice cover along with the lengthening of the ice free period in summer permit the opening of the Northwest Passage to navigation and potential hydrocarbon exploitation. This supports increasing economic interest in the Canadian Arctic. The eventual impacts of climate change and anthropogenic activities on benthic marine ecosystems can be severe, but are difficult to evaluate and predict, because few reference data documenting present conditions of this ecosystem exist. The general objective of this thesis is therefore to describe the diversity and the distribution of benthic communities of the Canadian Arctic, and to evaluate how environmental factors structure them. The first census of the diversity of megabenthic communities to this day at the Canadian Arctic scale (chapter 1) has enabled the study of environmental factors structuring them (chapter 2). Following this, a study at regional scale led to the creation of predictive models on the distribution of macrobenthos patterns (chapter 3). Finally, the spatial variability of benthic food-webs' functional responses along environmental gradients (chapter 4) has been examined in order to better understand the processes generating the environment – communities relationships described in the first three chapters.

First of all, chapter 1 demonstrates that 527 taxa of the megafauna have been identified out of 78 stations across the Canadian Arctic. The mean taxonomic richness observed in five Canadian Arctic regions are overall similar but it is predicted that there are 34 % to 59 % of taxa remaining to be documented in each region. Despite a high habitat heterogeneity (*beta* diversity), the Amundsen Gulf region showed a lower taxonomic richness than in the neighboring region of the Beaufort Sea. Megabenthic communities are overall similar across regions, except in the case of the Beaufort Sea region, where the Mackenzie River influences distinctively the community composition.

Chapter 2 shows that, at the Canadian Arctic scale, it is a combination of environmental factors at different spatial scales (continental, regional and local) which structure the six megafaunal benthic communities defined on the base of their taxonomic composition similarities. Overall, biomass, density and megafaunal richness decrease with depth and increase with food supply proxies. However, strength of all the statistical relationships analyzed was moderate, because local- to regional-scale physical and biological conditions, such as the presence of polynyas or of deep currents, interfere with continental-scale trends.

Chapter 3 looks specifically at environmental factors structuring communities of benthic macrofauna in the Beaufort Sea and Amundsen Gulf, regions where the exploration and exploitation of hydrocarbon sources are expected to intensify in the near future. Low temporal variability of communities has allowed assembling several databases from various scientific programs between 1973 and 2012 in order to create predictive models. Patterns of richness and density, as well as communities, are distributed regionally as a function of depth and salinity. At a finer scale on the continental shelf (< 200 m), communities are distributed in function of sediment grain size.

Finally, via the assessment of spatial variability of stable isotope composition of carbon ($\delta^{13}C$), chapter 4 indicates that the principal source of carbon for benthic invertebrates in the Canadian Arctic Archipelago originates from ice algae. This strong ice algae – benthos coupling is particularly evident in Barrow Strait and Eclipse Sound, two areas across the Canadian Arctic where highest ice algal biomass has been recorded until now. The variability of the nitrogen stable isotope composition ($\delta^{15}N$) demonstrates that, compared to their counterparts on the continental shelf (< 200 m), benthic primary consumers of deep stations (≥ 200 m) assimilate degraded organic matter and predator-scavenger feeders have principally an omnivorous diet.

This thesis overall provides numerous benthic baseline data for the Canadian Arctic, such as a census on megafauna benthic diversity. This research has also demonstrated the complexity of environment – community relationships acting at several spatial scales and brings new knowledge about the current importance of ice algae as a principal carbon source for Canadian Arctic benthic communities. Results on the principal environmental factors structuring community diversity and distribution could serve to identify ecologically and biologically significant areas (EBSAs), as well as in national designation process of marine protected areas and conservation strategies. Also, these results will assist to orient future scientific studies having as a goal a deeper understanding of processes and mechanisms of the relations identified in this thesis.

Keywords: Canadian Arctic, benthos, macrofauna, megafauna, diversity, community ecology, environmental variables, spatial variability, stable isotopes, pelagic-benthic coupling.

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INTRODUCTION GÉNÉRALE

De grands changements climatiques sont déjà en cours dans l'océan Arctique et devraient se poursuivre en réponse au réchauffement climatique global (ex. augmentation de la température de surface de l'océan, baisse de la couverture de glace, érosion côtière ; ACIA 2004). Les impacts actuels et futurs des changements climatiques sur l'écosystème marin benthique peuvent être sévères, mais sont difficiles à évaluer et à prévoir, car peu de données de référence documentant les conditions passées et actuelles de la diversité benthique arctique existent (Wassmann *et al.* 2011). Plusieurs théories prédisent une baisse du fort couplage pélago-benthique actuel qui soutient de grandes richesses et biomasses benthiques dans plusieurs régions de l'Arctique (Carroll & Carroll 2003 ; Piepenburg 2005 ; Bluhm & Gradinger 2008). Afin de protéger l'intégrité écologique de ces points chauds de richesse et de biomasse (« *hotspots* »), il faut d'une part les repérer et les décrire, et d'autre part comprendre comment divers facteurs environnementaux variant à diverses échelles spatiales et temporelles structurent actuellement la diversité et la distribution des communautés benthiques.

LA DIVERSITÉ BIOLOGIQUE, UN TERME AUX SENS MULTIPLES

La biodiversité joue plusieurs rôles, tant au niveau environnemental, social, économique, scientifique, culturel que récréatif. Elle influence le fonctionnement des écosystèmes et rend de multiples services à l'humanité (Hooper *et al.* 2005). Selon la définition de la Convention sur la diversité biologique des Nations Unies de 1992, la diversité des organismes vivants est divisée en trois composantes principales, soit la diversité au sein des espèces (intraspécifique, diversité génétique), entre les espèces (interspécifique, diversité spécifique) et à l'échelle des écosystèmes (diversité écosystémique). En écologie, on mesure généralement la diversité interspécifique, ou simplement nommée la diversité spécifique, au sein d'une communauté ou d'une région échantillonnée. Un autre type de diversité non inclus dans la définition de la Convention sur la diversité biologique des Nations Unies de 1992, mais de plus en plus étudié sera également traité ici, c'est-à-dire la diversité fonctionnelle (Petchey & Gaston 2006). Ces deux types de diversité ainsi que les moyens utilisés pour les mesurer dans cette thèse sont expliqués ici-bas.

Diversité spécifique

La diversité spécifique fait référence ici aux mesures classiques de diversité qui tiennent compte de la richesse en espèces ou en taxa d'une communauté. Les caractéristiques primaires d'une communauté, qui sont les plus simples à mesurer, sont la richesse (nombre d'espèces ou de taxa), l'abondance (nombre d'individus), la densité (nombre d'individus m^{-2}), la masse (ex. g) et la biomasse (ex. g m^{-2}) (Clarke & Warwick 2001 ; Gray & Elliott 2009). Les indices de diversité plus complexes, nommés aussi caractéristiques secondaires de la communauté, tiennent compte à la fois du nombre d'espèces (richesse) et du nombre d'individus par espèce (abondance). Il existe plusieurs indices de diversité secondaires que l'on distingue entre indices univariés et multivariés. Les indices de Shannon-Wiener (H'), de Simpson (D) et de Pielou (J') font partie des indices univariés les plus utilisés. Un indice univarié de diversité moins utilisé, l'indice de diversité taxonomique moyenne (Δ), considère les relations taxonomiques (degré de parenté entre deux taxa dans la classification hiérarchique linnéenne) et est par conséquent une mesure plus sensible de la structure des communautés, surtout dans une situation où l'abondance et la richesse spécifique restent stables alors que la composition spécifique, elle, change (Clarke & Warwick 2001). Parmi les indices multivariés, on dénote les méthodes de groupement et d'ordination utilisant des matrices d'association à partir de mesures de similarité ou de distance (ex. distance de Bray-Curtis). Les analyses multivariées sont particulièrement appropriées pour examiner les changements de composition spécifique et de dominance le long de gradients environnementaux ou de pollution (ex. gradient de matière organique, d'oxygène, de profondeur) (Gray & Elliott 2009).

Lorsque l'on s'intéresse à la variation de la composition en espèces entre les sites d'échantillonnage d'une région d'intérêt, cela fait généralement référence à la diversité *bêta* (β) (Magurran 2004 ; Gray & Elliott 2009). Le terme de diversité β a surtout été développé par Robert Harding Whittaker qui l'a défini comme étant le ratio de la richesse à une grande échelle (diversité *gamma,* γ) sur la moyenne des richesses de chaque site échantillonné (moyenne des diversités *alpha,* α) (Whittaker 1972). Il existe maintenant plusieurs autres méthodes de mesure de la diversité β (Magurran 2004 ; Anderson 2011), mais dans la majorité des cas on attribue une diversité β élevée à une grande hétérogénéité de l'environnement ou de l'habitat dans lequel vivent les communautés (Gray & Elliott 2009).

Diversité fonctionnelle

Un autre type de mesure de diversité qui gagne en popularité depuis les dix dernières années est la diversité fonctionnelle. D'une manière générale, Petchey & Gaston (2006) la définissent comme étant la diversité des fonctions que les organismes d'une communauté remplissent, soit les traits fonctionnels, par opposition à leur histoire évolutive qui définit la diversité spécifique. Les traits fonctionnels sont une composante du phénotype des organismes (Hillebrand & Matthiessen 2009) et décrivent par exemple la façon dont un organisme assimile l'énergie, c'est-à-dire le mode d'alimentation (ex. suspensivore contre déposivore), ou décrivent leur taux d'activité (ex. demande en oxygène).

Ce bref aperçu de mesures de diversité biologique illustre la « richesse » des méthodes utilisées pour définir la biodiversité. Aucune mesure de diversité biologique ne résume à elle seule la complexité biologique d'une communauté. C'est davantage l'évaluation simultanée de toutes ces mesures qui apporte une vision à la fois globale et nuancée de l'état de la biodiversité.

FACTEURS STRUCTURANT LA DIVERSITÉ ET LA DISTRIBUTION DES COMMUNAUTÉS BENTHIQUES

Les communautés benthiques dont il est question dans cette thèse incluent les invertébrés appartenant aux classes de taille de la macrofaune (≥ 0.5 mm) et mégafaune (≥ 1-2 mm). Les communautés de poissons de fond ne sont pas traitées. La macrofaune comprend principalement des organismes de l'endofaune échantillonnés au moyen de carottiers à boîte ou de bennes, tandis que la mégafaune inclut principalement de grands organismes de l'épifaune qui sont échantillonnés au moyen d'engins traînants tels que des chaluts, ou visibles sur les images et vidéos (Piepenburg 2005).

La diversité spécifique et fonctionnelle, mais également la distribution des communautés benthiques sont modulées à la fois par des facteurs abiotiques et biotiques. La disponibilité des ressources, l'environnement physico-chimique à la base de la colonne d'eau et la localisation spatiale (ex. profondeur) comptent parmi les facteurs abiotiques. Les facteurs biotiques, quant à eux, font référence aux interactions entre les organismes, notamment la compétition et la prédation (Gray & Elliott 2009). En raison de sa longévité et de sa faible mobilité, le benthos est considéré comme un bon intégrateur des conditions environnementales (Snelgrove & Butman 1994 ; McArthur *et al.* 2010). Sa diversité et sa distribution sont donc le fruit de l'influence, directe ou indirecte, d'une multitude de facteurs environnementaux.

Types de gradients environnementaux

Suivant la nomenclature de McArthur *et al.* (2010), les facteurs environnementaux peuvent être regroupés en trois grands gradients : des ressources, directs et indirects/spatiaux (Figure 1).

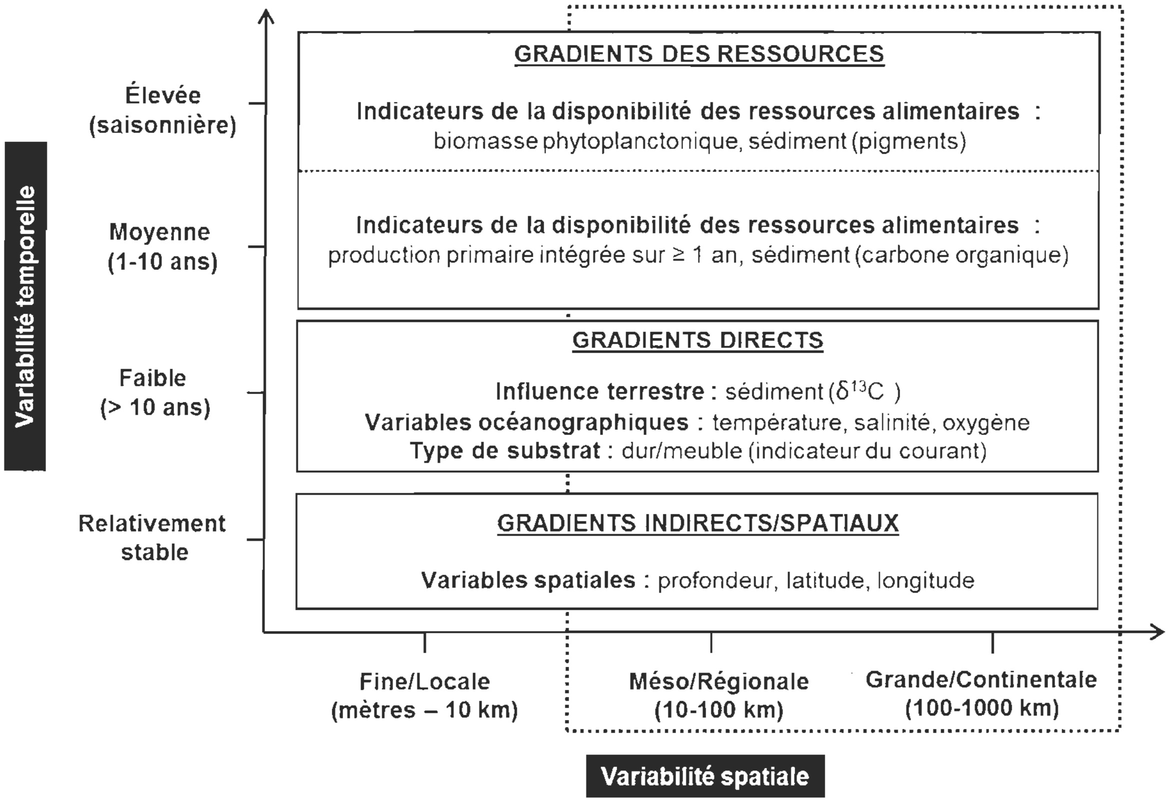


Figure 1. Échelles de variabilité spatiale et temporelle de certains facteurs environnementaux utilisés dans cette thèse. Les facteurs environnementaux sont divisés en trois grands types de gradients suivant la nomenclature de McArthur *et al.* (2010). L'encadré en pointillé en arrière-plan illustre que le plan d'échantillonnage de la présente étude permet d'étudier le rôle des facteurs environnementaux selon leur variabilité au niveau des échelles spatiales régionale et continentale.

Gradients des ressources

Les gradients des ressources incluent d'une part les variables qui estiment les flux verticaux de carbone organique particulaire (COP) à partir de données de production biologique dans les eaux de surface (ex. biomasse du phytoplancton, production primaire) et d'autre part les variables sédimentaires (ex. contenus en pigments, en carbone organique) qui indiquent plus directement les ressources alimentaires disponibles aux organismes benthiques. Toutes ces variables indicatrices de la disponibilité en nourriture seront appelées ci-après « indicateurs de la disponibilité des ressources alimentaires » (« *food* *supply proxies* »). Par exemple, de manière générale, un apport régulier et non excessif de ressources alimentaires a un effet positif sur la richesse, densité et biomasse des communautés benthiques (Gray 2002 ; McArthur *et al.* 2010).

Gradients directs

Les gradients directs englobent les facteurs qui ont une influence directe sur la physiologie et/ou la morphologie et/ou l'histoire évolutive d'une espèce. En font partie notamment les variables océanographiques à la base de la colonne d'eau (ex. température, salinité, oxygène), le type de substrat (ex. substrat dur ou meuble) et certaines variables indicatrices de l'influence terrestre par un apport de matière organique terrestre ou par l'érosion côtière (ex. valeurs faibles en $\delta^{13}C$ dans les sédiments). Par exemple, les invertébrés benthiques ayant un mode d'alimentation suspensivore et étant peu mobiles dominent généralement sur les substrats durs où il y a de forts courants, alors qu'une majorité d'invertébrés déposivores et mobiles peuplent les substrats meubles (Snelgrove & Butman 1994 ; McArthur *et al.* 2010).

Gradients indirects/spatiaux

Finalement les gradients indirects/spatiaux renferment les variables spatiales (ex. profondeur, latitude, longitude) qui n'ont aucune influence directe sur la physiologie des espèces. Les variables spatiales sont toutefois d'une grande utilité dans les études en écologie, car elles sont souvent corrélées à la fois aux variables des gradients directs et des ressources, et dans ce sens reflètent globalement l'importance d'une multitude de variables à la fois. Le rôle englobant des variables spatiales les rend toutefois difficiles à interpréter si elles sont les seules considérées en raison de leur influence indirecte sur les espèces et les communautés. Par exemple, à l'échelle globale, la richesse, la densité, la biomasse et la taille des individus diminuent avec la profondeur. Ces dernières relations sont en majorité liées à une baisse de la disponibilité des ressources alimentaires avec une augmentation de la profondeur (Rex *et al.* 2006), mais peuvent être liées aussi à de plus faibles concentrations en oxygène dans les eaux profondes (Levin *et al.* 2001).

Échelles de variabilité des facteurs environnementaux

Les gradients environnementaux et les variables qui les définissent manifestent une hétérogénéité mesurable à différentes échelles spatiales et temporelles (Whittaker *et al.* 2001) (Figure 1).

Les variables indicatrices de la disponibilité des ressources fluctuent soit sur une base saisonnière (ex. pigments dans les sédiments ; Morata *et al.* 2008) ou sur une base annuelle (ex. carbone organique dans les sédiments ; Magen *et al.* 2010 ; Bailey *et al.* 2013). Parmi les variables d'influence directe, les variables océanographiques mesurées à la base de la colonne d'eau en zones profondes sont considérées comme relativement stables sur une décennie (Michel *et al.* 2006). Les variables spatiales sont considérées comme stables dans la fenêtre temporelle où l'on effectue des études sur des données biologiques contemporaines.

Au niveau de leurs variabilités spatiales, les gradients environnementaux manifestent une hétérogénéité mesurable à toutes les échelles spatiales. Leur échelle spatiale d'influence dépendra de la résolution avec laquelle on les mesure, de la distance entre les sites d'échantillonnage et de l'étendue totale de l'aire d'étude (Whittaker *et al.* 2001). Néanmoins, d'une manière générale, les gradients des ressources ont davantage d'influence sur les échelles locale et régionale, alors que les gradients directs et indirects/spatiaux ont une influence significative sur l'écosystème benthique sur des échelles régionale à continentale (Piepenburg 2005).

L'ÉCOSYSTÈME BENTHIQUE ARCTIQUE

L'environnement marin arctique

L'océan Arctique, incluant ses mers épicontinentales, couvre une superficie de près de 14 x 10^6 km^2 (Carroll & Carroll 2003) (Figure 2). Les mers arctiques sont parmi les régions marines ayant les conditions climatiques les plus extrêmes sur Terre. La faune marine doit faire face à l'extrême saisonnalité de la lumière, de la salinité et de la présence de glace, et à l'année doit composer avec une température de l'eau proche du point de congélation (Gradinger *et al.* 2010). La présence de glace permanente (multiannuelle) et saisonnière, ainsi que les grands apports saisonniers d'eau douce et de nutriments en provenance des rivières, ont une profonde influence sur les processus physiques, biologiques et biogéochimiques de l'écosystème marin arctique (Carroll & Carroll 2003). Les écosystèmes pélagiques de haute latitude sont caractérisés par des cycles saisonniers de production primaire en raison de la variabilité de la disponibilité de la lumière et des nutriments pour la photosynthèse. Les floraisons d'algues de glace et de phytoplancton résultent en une contribution saisonnière importante de matière organique pour les compartiments pélagique et benthique (Figure 3). Les communautés benthiques arctiques peuvent être très productives lorsqu'elles sont couplées étroitement avec la production biologique pélagique. Par exemple, les fortes biomasses benthiques de la mer de Chukchi profitent à de nombreux oiseaux et mammifères marins qui visitent saisonnièrement cette région Arctique pour s'alimenter (Grebmeier *et al.* 2006 ; Bluhm & Gradinger 2008).

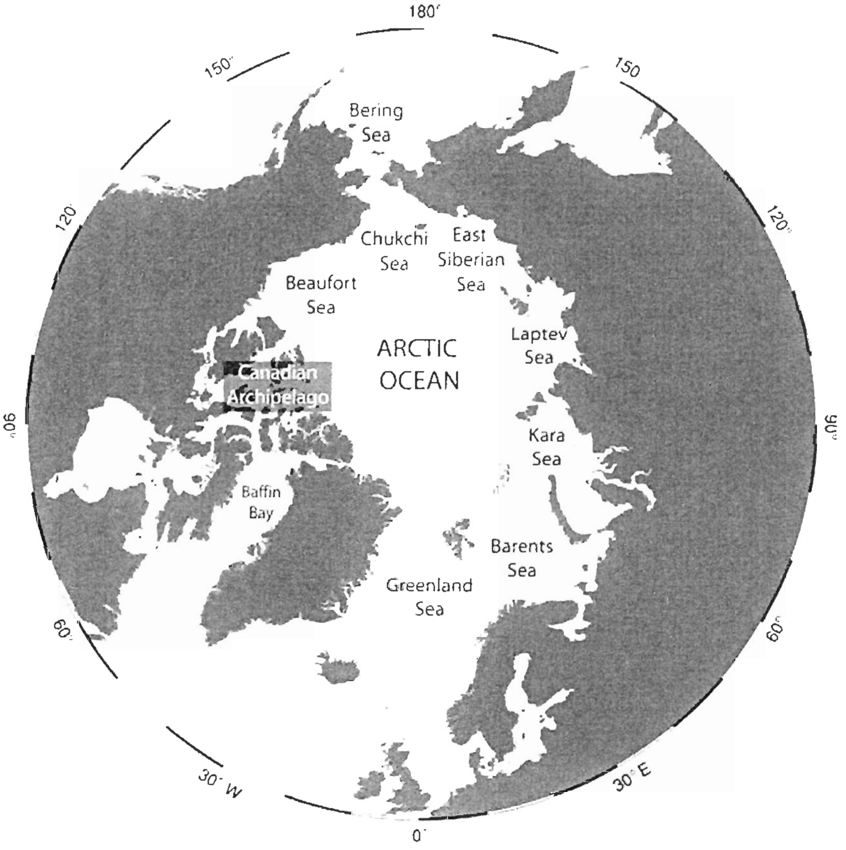


Figure 2. Carte de l'océan Arctique et de ses mers épicontinentales. Image tirée de Piepenburg (2005).

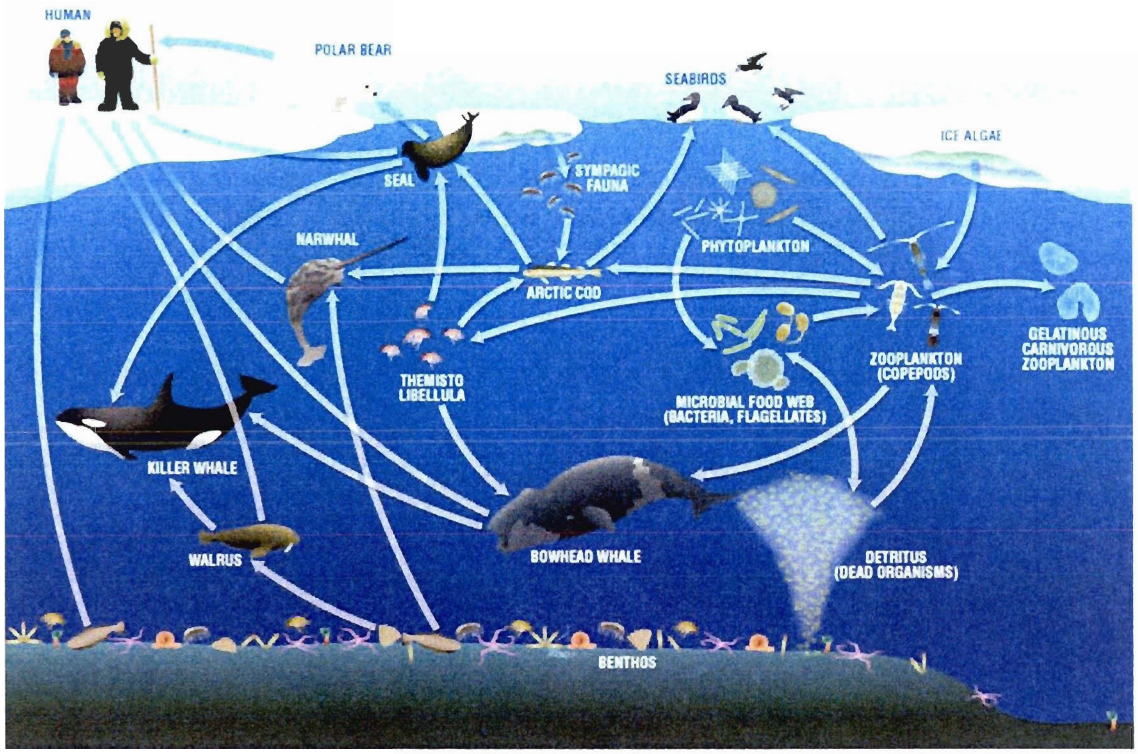


Figure 3. Les trois grands compartiments de l'écosystème marin arctique : la glace, la colonne d'eau et le fond marin. Ces compartiments sont en partie couplés entre eux par les flux de carbone. Image tirée de Darnis *et al.* (2012).

Le couplage pélago-benthique

Dans une comparaison latitudinale de partitionnement des flux d'énergie, le compartiment benthique reçoit plus d'énergie du compartiment pélagique en Arctique qu'en zones tempérées et tropicales en raison du fort couplage pélago-benthique actuellement existant dans plusieurs régions de l'océan Arctique (Bluhm & Gradinger 2008). Les mers épicontinentales peu profondes (< 100 m en moyenne ; ex. mer de Chukchi, zones côtières de la mer de Barents), les zones lisières des glaces et les polynies sont, généralement, caractérisées par un fort couplage pélago-benthique, comparativement aux endroits plus profonds du centre de l'océan Arctique (ex. bassins canadien et eurasien) (Piepenburg 2005). Néanmoins, de nouvelles données montrent que l'intensité du couplage pélago-benthique a été sous-estimée dans le centre de l'océan Arctique (Boetius *et al.* 2013). Le degré et la nature du couplage pélago-benthique varient grandement régionalement et résulteraient du produit de plusieurs facteurs, dont : les processus physiques qui contrôlent la stratification, la couche de mélange des eaux et les concentrations en nutriments pour la production primaire, la biomasse et la composition spécifique des algues de glace et du phytoplancton, la composition spécifique et l'efficacité du broutage du zooplancton, l'intensité de la boucle microbienne, et la profondeur de la colonne d'eau qui illustre indirectement l'atténuation des flux verticaux de COP (Wassmann 1998 ; Dunton *et al.* 2005 ; Bluhm & Gradinger 2008). Par conséquent, toute perturbation qui change la magnitude et la synchronie de ces évènements physiques et biologiques a un impact probable sur l'intensité du couplage pélago-benthique en Arctique. Par exemple, plusieurs études proposent que la fonte précoce de la glace annuelle favorisera un couplage phytoplancton – zooplancton au lieu du fort couplage algues de glace – benthos qui est typique actuellement dans plusieurs mers épicontinentales de l'Arctique (Figure 4) (Carroll & Carroll 2003 ; Piepenburg 2005 ; Arrigo *et al.* 2008; Bluhm & Gradinger 2008 ; Wassmann & Reigstad 2011). En effet, même si les algues de glace ne représentent qu'une faible fraction de la production primaire totale (environ de 3 à 30 %; Carmack *et al.* 2006), elles constituent une importante partie du COP qui est exporté vers les communautés benthiques à la fin du printemps, lors de la fonte de la glace (Grebmeier *et al.* 1995 ; Grebmeier *et al.* 2006). Puisque la croissance du zooplancton est limitée par la température de l'eau au printemps et par la nourriture durant l'été (Coyle & Pinchuk 2002), les températures plus chaudes prévues dans le futur et l'augmentation prédite de la production primaire pélagique pourraient entraîner une augmentation de près du double ou même plus de la production du zooplancton et donc limiter le flux direct de COP vers le benthos (Overland & Stabeno 2004). Par conséquent, la transition générale anticipée d'un couplage algues de glace – benthos vers un couplage phytoplancton – zooplancton dans les mers épicontinentales de l'océan Arctique aura un grand impact sur les communautés benthiques et il est donc attendu globalement que les prédateurs d'organismes benthiques (ex. morses, phoques barbus) seront désavantagés par rapport aux prédateurs pélagiques (ex. poissons, baleines, oiseaux) (Carroll & Carroll 2003 ; Carmack & Wassmann 2006 ; Bluhm & Gradinger 2008).

En raison de la forte saisonnalité de la production primaire et de son exportation hors de la zone euphotique en Arctique, la force du couplage pélago-benthique et son influence sur la disponibilité des ressources alimentaires pour les communautés benthiques, et conséquemment sur la distribution et les réponses fonctionnelles de ces dernières, sont au cœur de plusieurs études.

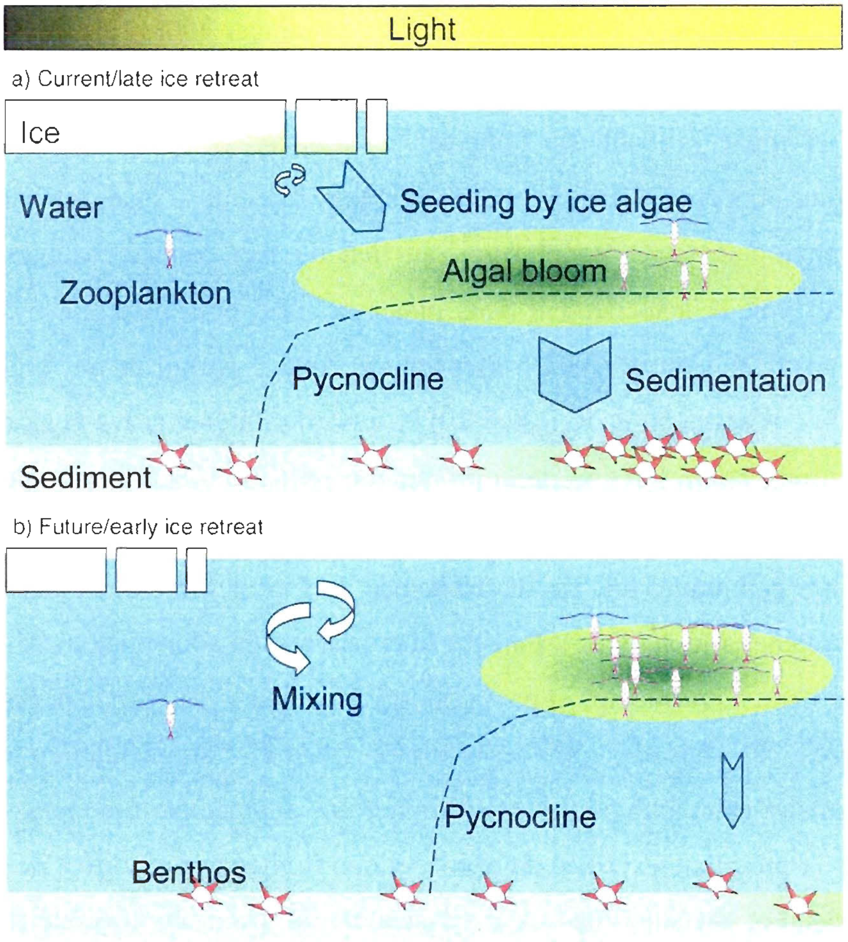


Figure 4. Représentation schématique du cycle saisonnier de la production primaire et de son exportation vers le fond marin. (**a**) État actuel avec une forte exportation de COP vers le benthos. (**b**) État théorique futur où la fonte précoce de la glace permettra un brassage de la colonne d'eau plus important et retardera la stratification nécessaire à l'établissement de la floraison du phytoplancton à un moment qui coïncidera avec la présence de grandes densités de zooplancton, réduisant conséquemment le flux de COP vers le benthos. Image tirée de Bluhm & Gradinger (2008).

État des connaissances du contrôle environnemental sur les communautés benthiques de l'Arctique

Gradients des ressources - Indicateurs de la disponibilité des ressources alimentaires

En raison de la complexité des interactions biologiques et physiques qui peuvent augmenter ou réduire le couplage pélago-benthique, divers indicateurs de la disponibilité des ressources alimentaires, intégrant une variabilité saisonnière ou annuelle, sont utilisés pour interpréter les réponses de l'écosystème benthique arctique (Figure 1). Selon Klages *et al.* (2004), la disponibilité de la nourriture est le facteur qui détermine le plus la structure et le fonctionnement des communautés benthiques des marges continentales de l'Arctique canadien, et ce, pour tous les spectres de taille du benthos, de la microfaune à la mégafaune. Néanmoins, sur une échelle temporelle, les différents compartiments de taille du benthos et la gamme variée de réponses mesurées sur les communautés ne répondent pas tous à la même vitesse à la variabilité des ressources alimentaires. Par exemple, les plus petites tailles de classe (microfaune, méiofaune) répondent généralement plus rapidement à une arrivée soudaine de phytodétritus au fond que les tailles plus grandes (macrofaune et mégafaune) (Klages *et al.* 2004). D'autre part, suivant qu'on étudie les fonctions d'une communauté benthique ou sa structure, l'échelle de temps de réponse diffère : la demande en oxygène de la macrofaune augmente saisonnièrement avec l'arrivée de phytodétritus au fond (Renaud *et al.* 2007b ; Link *et al.* 2011), alors que les caractéristiques et la structure des communautés de la macrofaune (ex. biomasse, abondance, composition) intègrent la variabilité de la disponibilité des ressources sur des décennies, voire même plus (Carroll *et al.* 2008). En effet, la macro et mégafaune benthique des hautes latitudes ont une grande longévité et sont relativement sessiles (Carroll *et al.* 2008), et par conséquent les caractéristiques et la structure de leurs communautés reflètent des réponses intégratives sur le long terme.

L'atténuation des flux de COP atteignant le fond peut limiter grandement la disponibilité des ressources alimentaires aux communautés benthiques (Grebmeier & Barry 1991 ; Wassmann 1998), et donc tout indicateur reflétant le mieux la disponibilité des ressources directement sur le fond marin aura potentiellement un grand pouvoir explicatif de la structure des communautés benthiques. Ainsi, les indicateurs de la disponibilité des ressources alimentaires dans les sédiments de surface (ex. concentration des pigments, contenu en carbone organique) sont généralement bien corrélés avec la biomasse et densité des communautés benthiques arctiques (Grebmeier *et al.* 2006 ; Carroll *et al.* 2008 ; Cochrane *et al.* 2009 ; Carroll & Ambrose 2012). Dans les régions où de manière récurrente de fortes productions primaires sont jumelées à de forts flux d'exportation de COP, les indicateurs de productivité primaire en surface (biomasse, production primaire) sont également bien corrélés avec la biomasse et densité des communautés benthiques (Carroll *et al.* 2008 ; Cochrane *et al.* 2009 ; Carroll & Ambrose 2012).

Il existe toutefois des manières plus approfondies de mesurer la force du couplage pélago-benthique afin de définir plus directement la source de nourriture assimilée par les organismes benthiques. Outre l'analyse fastidieuse des contenus stomacaux, les analyses plus rapides de la composition des isotopes stables du carbone ($\delta^{13}C$) et des acides gras sont de plus en plus utilisées dans les études arctiques. Les études utilisant les isotopes stables suggèrent en général qu'il existe un fort couplage pélago-benthique, que ce couplage soit majoritairement dérivé des algues de glace (Søreide *et al.* 2013) ou du phytoplancton (Tamelander *et al.* 2006a ; Iken *et al.* 2010 ; Carroll *et al.* 2014). Par ailleurs, d'autres études ont montré que les communautés benthiques pourraient s'alimenter majoritairement sur du matériel dégradé par le réseau microbien sédimentaire (Lovvorn *et al.* 2005 ; McTigue & Dunton 2013). Toutes ces dernières études se sont concentrées aux environnements de moins de 200 m de profondeur et très peu d'études en Arctique ont analysé la variabilité spatiale des compositions en isotopes stables des invertébrés benthiques le long de gradients de profondeur et à des stations de plus de 200 m (Iken *et al.* 2005 ; Bergmann *et al.* 2009). D'ailleurs, aucune étude à ce jour n'a entrepris une vaste analyse spatiale de la force du couplage pélago-benthique le long du gradient de profondeur et des régimes de production biologique dans l'Arctique canadien.

Gradients directs - Variables océanographiques

Les variables océanographiques font référence ici aux variables mesurées à la base de la colonne d'eau, telles que la salinité, la température, la concentration en oxygène et font aussi référence aux courants de fond.

Lorsque l'on considère uniquement les communautés benthiques des zones au large ou profondes des plateaux continentaux arctiques, la variabilité régionale et continentale des variables océanographiques coïncide de manière générale avec le partitionnement des masses d'eau. La variabilité spatiale des communautés benthiques est ainsi fortement corrélée aux variables océanographiques et par conséquent aux masses d'eau dans plusieurs mers épicontinentales de l'océan Arctique, par exemple dans la mer de Barents (Carroll *et al.* 2008), la mer du Groenland (Mayer & Piepenburg 1996) et la mer de Chukchi (Ravelo *et al.* 2013) (Figure 2). Aucune de ces études n'a pu définir le rôle direct des masses d'eau dans la structure des communautés, et c'est fort possiblement l'interaction de plusieurs facteurs, dont les préférences physiologiques des organismes (Levin *et al.* 2001), l'influence des masses d'eau sur la production primaire (Bluhm *et al.* 2009), les migrations postglaciaires des espèces atlantiques et pacifiques sur les plateaux continentaux de l'océan Arctique (Dunton 1992), qui font des variables océanographiques des facteurs environnementaux hautement explicatifs des patrons de distribution des communautés benthiques arctiques.

Les courants ne sont pas limités aux eaux de surface et peuvent être observés de façon transitoire ou permanente à n'importe quelle profondeur, particulièrement près de pentes abruptes et en présence de structures topographiques, telles que les fosses sous-marines (« *trough* »). Les courants au-dessus des fonds marins sont un facteur important modulant à la fois la distribution du type de substrat sédimentaire et l'advection latérale de matériels organiques, et donc influencent directement les communautés benthiques (Snelgrove & Butman 1994). Comme dans toute région marine mondiale, la composition spécifique et la structure trophique des communautés benthiques de l'océan Arctique varient entre substrats meuble et dur, avec une dominance de suspensivores sur substrat rocheux ou dur et avec une dominance de déposivores sur substrat meuble (Mayer & Piepenburg 1996 ; Bluhm *et al.* 2009). Le plus faible courant profond peut excéder la vitesse de chute des particules du plancton par au moins un ordre de grandeur (Klages *et al.* 2004) et ainsi le transport latéral de matériels organiques peut être significatif pour les communautés benthiques, en particulier celles vivant en eaux profondes. Aux échelles locale et régionale, il est également reconnu que les zones de remontée d'eau profonde affectent généralement positivement les communautés benthiques en Arctique par leur action en cascade sur la production primaire et sur les flux de COP hors de la zone euphotique (Conlan *et al.* 2013). La topographie du fond marin à une échelle locale peut également influencer la circulation de l'eau et ainsi favoriser un apport accru de COP localement, sans que cette influence puisse être détectable à l'échelle régionale (Blanchard & Feder 2013).

Gradients indirects/spatiaux – Profondeur, latitude et longitude

Les études sur les communautés benthiques arctiques en zones profondes (> 200 m) sont rares comparativement aux études plus nombreuses effectuées sur les plateaux continentaux (< 200 m). Néanmoins, les conclusions générales des études existantes montrent que les caractéristiques (ex. densité, biomasse) et la distribution des communautés benthiques suivent une zonation corrélée avec la profondeur, concordant ainsi avec les relations observées dans d'autres régions marines du monde. Les études passées ont examiné à la fois les patrons des communautés benthiques le long de gradient de profondeur du plateau vers la pente continentale (Mayer & Piepenburg 1996 ; Piepenburg *et al.* 1996 ; Conlan *et al.* 2008), et de la pente continentale vers la zone abyssale (> 2 000 m) (Bluhm *et al.* 2005 ; Soltwedel *et al.* 2009 ; MacDonald *et al.* 2010). La zonation du plateau vers la pente continentale en Arctique est générée par divers facteurs environnementaux, et non par un seul facteur, dont la distance par rapport à l'embouchure d'une rivière, l'atténuation de la disponibilité en nourriture, l'histoire biogéographique, la granulométrie et les courants (Curtis 1975 ; Piepenburg 2005).

La latitude et la longitude sont des variables peu évaluées dans les études arctiques, car elles impliquent des aires d'étude couvrant de grandes étendues géographiques. La latitude et la longitude expliquent généralement significativement les patrons de diversité et de distribution des communautés benthiques à l'intérieur de zones géographiques où il y a un gradient de concentration de glace, de régimes de production primaire ou de courants (Carroll *et al.* 2008 ; Bluhm *et al.* 2009 ; Ravelo *et al.* 2013).

État des connaissances de la diversité et de la distribution des communautés benthiques dans l'Arctique canadien

En comparaison avec d'autres régions arctiques, telles que la mer de Barents, l'archipel de Svalbard et les mers de Béring et de Chukchi, les communautés benthiques de l'Arctique canadien n'ont pas été échantillonnées aussi intensément et depuis aussi longtemps. Pourtant, une grande diversité benthique y est prédite, car les campagnes d'échantillonnage dans l'Arctique canadien sont loin d'avoir recensé toutes les espèces attendues (Archambault *et al.* 2010). De plus, la très grande majorité des études en écologie benthique dans l'Arctique canadien ont été effectuées à l'échelle régionale et étudient généralement le compartiment de la macrofaune et traitent très peu des compartiments de la mégafaune et de la méiofaune (< 44-63 μm ; Giere 2009). De manière générale, la productivité benthique est plus faible dans l'Arctique canadien que dans les mers de Béring et de Chukchi (Grebmeier *et al.* 1995) et est spatialement variable. Actuellement, certaines régions de l'Arctique canadien ont de forts taux de sédimentation de COP vers le compartiment benthique, ce qui résulte en de fortes biomasses benthiques à ces endroits, comme dans le détroit de Lancaster (Thomson 1982) et au large du cap Bathurst (Conlan *et al.* 2013).

Les données sur la diversité de la macrofaune dans l'Arctique canadien sont disponibles depuis les années 1950 par le biais de rapports statistiques de Pêches et Océans Canada et de diverses études commandées par l'industrie pétrolière. De récents documents de synthèse ont compilé ces données dans le but de comparer la diversité de la macrofaune entre certaines régions géographiques de l'Arctique canadien (Stewart *et al.* 2001 ; Cusson *et al.* 2007 ; Chapman & Kostylev 2008 ; Archambault *et al.* 2010 ; Piepenburg *et al.* 2011). La plupart de ces données historiques ont été recueillies soit afin de documenter l'état de référence des communautés de la macrofaune ou plus spécifiquement pour étudier les impacts probables reliés aux activités anthropiques, en particulier en ce qui concerne l'exploitation des hydrocarbures. Au courant des années 1980-1990, des données additionnelles sur la diversité de la macrofaune ont été publiées dans le détroit de Lancaster (Thomson 1982) et dans la polynie des eaux du Nord par le biais du programme NOW (*International North Water Polynya Study* ; Lalande 2003). Les programmes scientifiques de recherche se sont intensifiés dans les années 2000 et notre compréhension des écosystèmes benthiques de l'Arctique canadien augmente depuis rapidement. Des campagnes intensives d'échantillonnage sur la diversité de la macrofaune ont été entreprises dans la mer de Beaufort et le golfe d'Amundsen par le biais des programmes CASES en 2003-2004 (*Canadian Arctic Shelf Exchange Study* ; Conlan *et al.* 2008 ; Conlan *et al.* 2013) et durant l'Année internationale polaire - Étude sur le chenal de séparation circumpolaire (*International Polar Year - Circumpolar Flaw Lead System Study* ; Forest *et al.* 2011 ; Link *et al.* 2011 ; Tremblay *et al.* 2011 ; Darnis *et al.* 2012) en 2007-2008. Finalement les campagnes d'échantillonnages dans le cadre du programme *Amundsen* des réseaux scientifiques ArcticNet et CHONe entre 2009 et 2011 ont permis d'amasser un grand nombre de données à travers une vaste étendue de l'Arctique canadien, de la mer de Beaufort jusqu'au nord de la baie de Baffin incluant des stations au cœur de l'archipel canadien. À la fois la diversité de la macrofaune (Link *et al.* 2013b) et de la mégafaune (Roy *et al.* 2014) ont été étudiées dans le cadre de ces dernières missions scientifiques.

Un survol des principales études benthiques effectuées dans l'Arctique canadien pour les communautés de la macrofaune et incluant seulement ou en majorité des sites sublittoraux et situés loin des côtes est présenté ici-bas.

À l'échelle de l'Arctique canadien

L'étude de Cusson *et al.* (2007) a recensé 947 taxa de la macrofaune benthique sur un total de 219 stations et a démontré une variabilité interrégionale de la richesse taxonomique et de la structure des communautés. Les auteurs ont observé une plus grande richesse spécifique taxonomique dans les régions à l'est de l'Archipel canadien qu'au centre et à l'ouest. Ils ont également constaté l'influence significative de grandes rivières, notamment la rivière Mackenzie et La Grande Rivière, sur la richesse taxonomique et la composition des communautés benthiques. La zone d'étude couvrait 15° de latitude, mais aucune tendance latitudinale n'a été observée.

L'étude de Link *et al.* (2013b) a recensé 311 taxa de la macrofaune benthique sur un total de 18 stations. L'étude a montré qu'il n'y avait pas de variabilité interannuelle de la composition taxonomique aux sites échantillonnés sur deux années consécutives.

À l'échelle régionale

Dans la mer de Beaufort et le golfe d'Amundsen, l'étude de Conlan *et al.* (2008) a recensé 497 taxa de la macrofaune benthique sur un total de 52 stations et a démontré que la profondeur influençait la composition taxonomique des communautés et que les plus fortes densités de macrofaune étaient situées dans la fosse du Mackenzie (« *Mackenzie trough* ») et au large du Cap Bathurst. L'étude de Conlan *et al.* (2013) a révélé une zone de fort couplage pélago-benthique s'étendant sur 4 550 km^2 à l'ouest du cap Bathurst où une remontée d'eau profonde (Williams & Carmack 2008) favorise la production primaire (Tremblay *et al.* 2011) et où de forts taux d'exportation de COP hors de la zone euphotique ont été enregistrés (Sallon *et al.* 2011 ; Forest *et al.* 2013). Ce fort couplage pélago-benthique résulte en une forte densité et biomasse de crustacés de la famille des Ampeliscidae, des proies de choix pour les baleines grises, dont les observations dans cette région se multiplient (Conlan *et al.* 2013).

Dans le détroit de Lancaster et la baie de Baffin, l'étude de Thomson (1982) a identifié 343 taxa de la macrofaune benthique sur un total d'environ 23 stations et a illustré l'impact du gradient de profondeur, des courants et de la production primaire sur la densité, la biomasse, la composition taxonomique et la dominance des guildes trophiques. L'auteur a observé que la biomasse et la densité diminuaient avec une augmentation de la profondeur. L'auteur a également remarqué de fortes biomasses benthiques et une dominance de suspensivores à l'entrée du détroit de Lancaster comparativement au centre de la baie de Baffin. Il a expliqué cette dernière différence par de plus forts courants ainsi que par une plus grande production primaire enregistrée dans le détroit de Lancaster comparativement au centre de la baie de Baffin.

Dans la polynie des eaux du Nord (NOW), située au nord de la baie de Baffin, l'étude de Lalande (2003) a recensé 120 taxa de la macrofaune benthique sur un total de quatre stations. L'auteur a défini trois communautés distinctes de l'est, du centre et de l'ouest de la polynie sur la base de la composition taxonomique et des guildes trophiques. La granulométrie et les patrons de courants profonds étaient les principaux facteurs structurant cette répartition spatiale des communautés.

OBJECTIF GÉNÉRAL DU PROJET

Dans le cadre d'une consultation scientifique nationale récente du secrétariat canadien de consultation scientifique (SCCS) de Pêches et Océans Canada, des zones d'importance écologique et biologique (ZIEB) à la grandeur de l'Arctique canadien ont été délimitées (DFO 2011). Il a été constaté que la couverture spatiale des données benthiques disponibles est limitée dans plusieurs régions. À ces endroits, nous devons nous rabattre sur des indicateurs potentiels de la production benthique pour en estimer la richesse et les fonctions (ex. la concentration en pigments dans les sédiments de surface, présence de polynies) (Kenchington *et al.* 2011). Toutefois, on utilise souvent ces indicateurs en se basant sur des études effectuées à l'extérieur de l'Arctique canadien et il y a par conséquent un besoin pressant de définir la force et l'échelle spatiale du contrôle environnemental sur la diversité et la distribution des communautés benthiques existant dans les eaux arctiques canadiennes.

Les trois objectifs globaux de cette thèse sont ainsi : (1) d'en faire une étude de référence en apportant de nouvelles données sur la diversité et la distribution des communautés benthiques de la macrofaune et mégafaune de l'Arctique canadien; (2) de déterminer comment les facteurs environnementaux structurent ces communautés benthiques; et (3) de transférer en partie les résultats aux instances gouvernementales, principalement Pêches et Océans Canada, afin d'enrichir l'état des connaissances des écosystèmes benthiques de l'Arctique canadien et d'appuyer la désignation de ZIEB.

Objectifs spécifiques

Plus spécifiquement la thèse est divisée en quatre chapitres qui présentent à différentes échelles spatiales (régionale contre continentale), divers compartiments benthiques (macrofaune contre mégafaune), selon différents types de diversité des communautés (spécifique contre fonctionnelle), et ce en utilisant différentes variables réponses de ces types de diversité (caractéristiques, distribution et structure des communautés contre guildes trophiques). Les chapitres de la thèse sont positionnés dans la Figure 5 ci-bas.

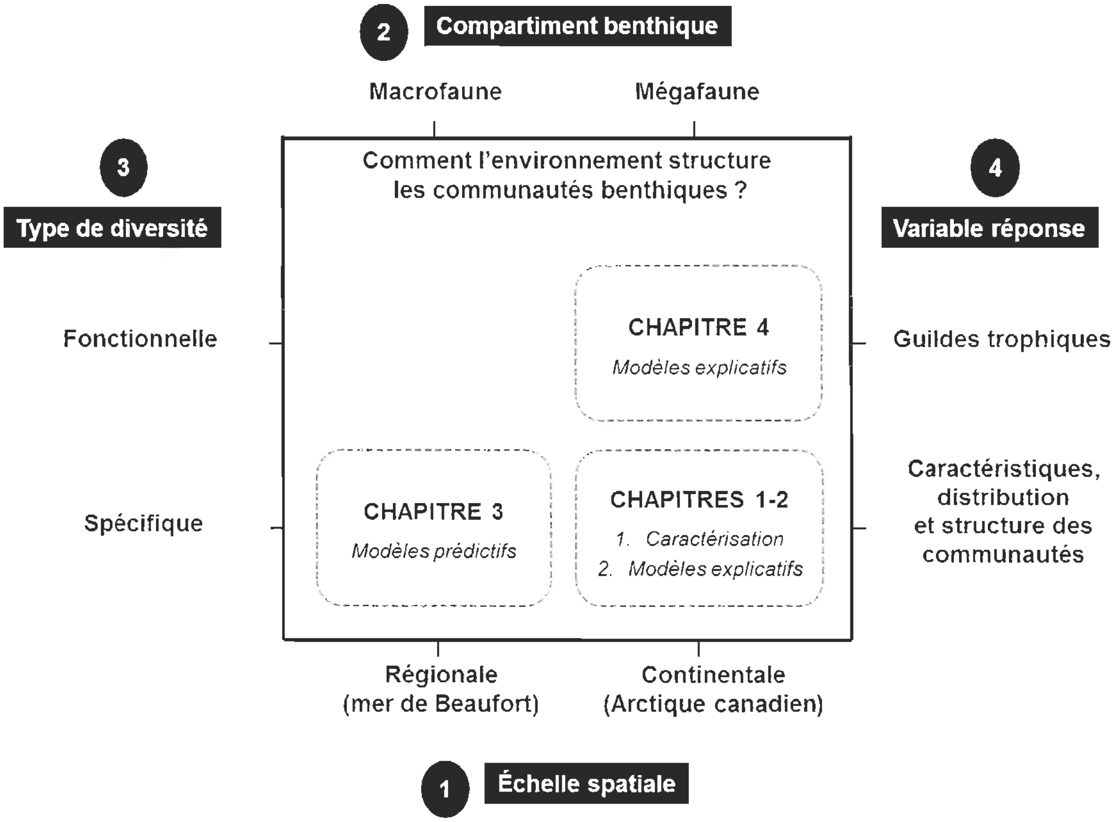


Figure 5. Vision globale des chapitres de la thèse selon (1) l'échelle spatiale étudiée, (2) le compartiment benthique analysé, (3) le type de diversité considéré, et (4) la variable réponse utilisée. La question centrale de cette thèse est de définir comment l'environnement structure les communautés benthiques de l'Arctique canadien.

Pour atteindre les objectifs globaux et réaliser les chapitres individuels, j'ai utilisé différentes approches scientifiques, c'est-à-dire une approche de caractérisation et des approches explicative et prédictive (Figure 5). Tout d'abord, la première caractérisation des communautés benthiques de la mégafaune à ce jour a permis de fournir un cadre de référence de cette diversité à l'échelle de l'Arctique canadien (chapitre 1). Dans un deuxième temps, au moyen de modèles statistiques explicatifs, j'ai déterminé à l'échelle de l'Arctique canadien la force des relations entre divers facteurs environnementaux et la distribution des communautés de la mégafaune (chapitre 2). En regard des connaissances acquises par les précédents modèles explicatifs, j'ai ensuite créé des modèles prédictifs pour la macrofaune à l'échelle régionale de la mer de Beaufort (chapitre 3). Finalement, j'ai utilisé des modèles explicatifs pour relier la variabilité spatiale des compositions isotopiques (carbone et azote) de guildes trophiques de la mégafaune à certains gradients environnementaux (chapitre 4). C'est ainsi la considération simultanée des résultats des différentes approches scientifiques utilisées dans cette thèse qui permet d'avoir une vision à la fois globale et nuancée du contrôle environnemental sur les communautés benthiques de l'Arctique canadien.

Chapitre 1 : Variabilité régionale de la structure des communautés de la mégafaune benthique à travers l'Arctique canadien

L'objectif principal du chapitre 1 est de recenser la composition taxonomique des communautés de la mégafaune benthique à l'échelle de l'Arctique canadien. Ce chapitre vise également à fournir des estimations de richesse observée et prédite pour cinq grandes régions de l'Arctique canadien : mer de Beaufort, golfe d'Amundsen, ouest et est de l'archipel canadien et la baie de Baffin. J'établis d'une part si les richesses recensées par grande région sont près ou loin des richesses prédites. D'autre part, je teste si les caractéristiques et la composition taxonomique des communautés de la mégafaune varient significativement entre les grandes régions à l'étude. Cette étude descriptive ne teste pas d'hypothèse particulière.

Le chapitre 1 constitue la première étude de référence de la composition taxonomique des communautés de la mégafaune benthique à l'échelle de l'Arctique canadien.

Chapitre 2 : Facteurs environnementaux structurant les communautés de la mégafaune benthique de l'Arctique canadien

Le chapitre 2 reprend les données de référence du chapitre 1 et a pour objectifs : (1) de délimiter des communautés sur la base de la similarité de leur composition taxonomique et de caractériser la structure et les patrons de distribution de ces communautés, et (2) d'évaluer l'influence de divers facteurs environnementaux sur les caractéristiques et les patrons de distribution des communautés. Je teste l'hypothèse que les caractéristiques des communautés (ex. biomasse, richesse) décroissent avec la profondeur, alors qu'elles augmentent avec les indicateurs de la disponibilité des ressources. J'émets également l'hypothèse que les principaux facteurs environnementaux expliquant la distribution des communautés sont surtout des facteurs associés à des gradients environnementaux variant à grande échelle (100-1000 km), et en importance moindre des facteurs associés à des gradients environnementaux régionaux (10-100 km). Considérant ces échelles spatiales, il est prévu que les principaux facteurs explicatifs feront partie en majorité des catégories de gradients directs et indirects/spatiaux.

Le chapitre 2 permet d'établir la force des relations environnement – communautés à l'échelle de l'Arctique canadien et démontre si de grandes tendances significatives émergent ou non à cette échelle spatiale.

Chapitre 3 : Modèles de prédiction de la distribution des communautés de la macrofaune benthique de l'est de la mer de Beaufort et du golfe d'Amundsen

Les deux principaux objectifs du chapitre 3 sont : (1) d'assembler toutes les bases de données disponibles de la macrofaune benthique dans la région de la mer de Beaufort et le golfe d'Amundsen entre 1973 et 2012 et (2) de créer des modèles prédictifs de la richesse, de la densité et de la distribution des communautés en fonction de facteurs environnementaux échantillonnés au moment de la collecte de la faune benthique. Je teste en premier lieu l'hypothèse centrale de cette étude qui considère que la variabilité spatiale des communautés benthiques à l'échelle de la région à l'étude surpasse la variabilité temporelle. Je teste ensuite l'hypothèse que la profondeur et les variables océanographiques sont des prédicteurs plus significatifs que les caractéristiques sédimentaires à l'échelle de la région à l'étude.

Le chapitre 3 permet de montrer s'il est envisageable d'assembler plusieurs bases de données collectées sur près de 40 ans à l'échelle régionale afin de produire des modèles prédictifs basés uniquement sur la variabilité spatiale.

Chapitre 4 : Réponses du réseau trophique benthique à la production biologique et à la profondeur dans l'Arctique canadien

Le chapitre 4 définit si et comment quatre guildes trophiques (les suspensivores, déposivores, suspensivores/déposivores facultatifs et les prédateurs-charognards) répondent aux gradients de profondeur et de production biologique de l'Arctique canadien en analysant la variabilité naturelle des compositions des isotopes stables du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$). Les principaux objectifs sont : (1) de déterminer si les mêmes facteurs environnementaux expliquent la variabilité spatiale des signatures isotopiques des sources alimentaires et des guildes trophiques, (2) d'évaluer si les consommateurs primaires ont une signature isotopique en carbone proche de celles des sources alimentaires disponibles au moment de l'échantillonnage, et (3) d'établir si la signature isotopique en azote des guildes trophiques change avec la profondeur. J'émets les hypothèses suivantes : (1) différents facteurs environnementaux expliquent la variabilité spatiale des sources de nourriture et des guildes trophiques, et (2) à la fois pour les sources de nourriture et les guildes trophiques, le gradient de production biologique influencera majoritairement la variabilité spatiale de la signature isotopique du carbone alors que le gradient de profondeur influencera principalement la variabilité spatiale de la signature isotopique en azote.

Le chapitre 4 donne une vision plus précise des processus par lesquels les gradients environnementaux influencent la nourriture assimilée par le benthos à travers une vaste zone de l'Arctique canadien.

CHAPITRE 1

VARIABILITÉ RÉGIONALE DE LA STRUCTURE DES COMMUNAUTÉS DE LA MÉGAFAUNE BENTHIQUE À TRAVERS L'ARCTIQUE CANADIEN

RÉSUMÉ

Des changements climatiques majeurs sont en cours dans l'Arctique canadien, mais notre capacité à surveiller et à prévoir leurs impacts sur la structure des communautés est entravé par le manque de données de référence sur la diversité. Cette étude combine des données sur les communautés mégabenthiques échantillonnées à 78 stations de 2007 à 2011 à l'intérieur des unités biogéographiques de l'Ouest et de l'Est de l'Arctique canadien. Ces grandes unités biogéographiques ont été divisées en cinq régions géographiques afin de fournir des estimations régionales de richesse taxonomique observée et prédite. Nous n'avons pas détecté de fortes différences régionales dans les caractéristiques des communautés. Seule la richesse observée est inférieure dans le golfe d'Amundsen par rapport à la région voisine de la mer de Beaufort. La région du golfe d'Amundsen a la diversité *bêta* la plus élevée, ce qui révèle une grande hétérogénéité d'habitat. La composition taxonomique de la mer de Beaufort est différente de celle des autres régions. La présence distinctive et forte de *Saduria* spp., un isopode euryhalin, dans la région de la mer de Beaufort illustre l'influence de la rivière Mackenzie sur la composition taxonomique de cette région. Notre analyse démontre que régionalement environ 34 % à 59 % des taxa restent à être documentés dans les eaux arctiques canadiennes. Cette étude fournit des données de référence utiles pour les objectifs nationaux et panarctique orientés sur l'évaluation de la diversité benthique de l'océan Arctique.

Ce premier article, intitulé « *Regional variability of megabenthic community structure across the Canadian Arctic* » fut corédigé par moi-même, les professeurs Katrin Iken et Philippe Archambault. L'article a été soumis le 23 juillet 2014 à la revue *Arctic*. En tant que première auteur, ma contribution à ce travail fut l'essentiel de la recherche bibliographique, l'échantillonnage, les analyses de laboratoire, le traitement statistique des résultats et la rédaction de l'article. Le professeur K. Iken a contribué à l'approche statistique et a aidé à la révision de l'article. Le professeur P. Archambault a contribué à l'idée originale, à l'approche statistique et a aidé à la révision de l'article. Une version abrégée de cet article a été présentée lors d'une *Consultation scientifique nationale du secrétariat canadien de consultation scientifique de Pêches et Océans Canada* en juin 2011 à Winnipeg (Canada).

REGIONAL VARIABILITY OF MEGABENTHIC COMMUNITY STRUCTURE ACROSS THE CANADIAN ARCTIC

ABSTRACT

Major climate changes are underway in the Canadian Arctic, but our ability to monitor and predict community structure changes are hindered by the lack of baseline diversity data. This study combined megabenthic community data sampled at 78 stations from 2007-2011 across the Western and Eastern Canadian Arctic biogeographic units. These large biogeographic units were divided into five geographical regions to provide regional estimates of observed and predicted taxon richness. We did not detect a strong regional difference in benthic community characteristics with lower observed richness only in the Amundsen Gulf region relative to the neighboring Beaufort Sea region. The Amundsen Gulf region had the highest turnover (*beta*) diversity suggesting high habitat heterogeneity. The community composition of the Beaufort Sea region was different than all other regions, characterized by the distinctive and strong presence of *Saduria* spp., a euryhaline isopod, that demonstrated the particular influence of the Mackenzie River on the community composition of that region. Our analysis demonstrated that regionally about 34 % to 59 % of megabenthic taxa are still to be documented in Canadian Arctic waters. This study provides useful baseline data for both national and pan-Arctic goals directed to evaluating the benthic diversity of the Arctic Ocean.

***Keywords*:** Canadian Arctic, benthos, megafauna, richness, community, Beaufort Sea, Amundsen Gulf, Canadian Archipelago, Baffin Bay.

INTRODUCTION

In the Arctic, major climate changes are already underway and are projected to continue in response to global warming (e.g., warming sea surface temperatures, coastal erosion; ACIA 2004). Arctic sea ice retreat during the summer is fueling increasing interest in the Canadian Arctic for the opening of the Northwest Passage and for oil exploration (Melling 2002; Rogers *et al.* 2013). Possible impacts of climate changes and anthropogenic activities on the Arctic benthic marine environment may be acute, but are difficult to assess and predict because extensive baseline data documenting present marine benthic ecosystem conditions are lacking (Wassmann *et al.* 2011). Research programs in the Canadian Arctic have increased in the last two decades (e.g., International North Water Polynya Study (NOW), Canadian Arctic Shelf Exchange Study (CASES), International Polar Year-Circumpolar Flaw Lead System Study (IPY-CFL), ArcticNet-CCGS *Amundsen* oceanographic expeditions), yet little is still known about megabenthic taxon richness across the large spatial extent of the Canadian Arctic.

The main objective of this study was therefore to assess the observed number of megabenthic taxa and predict the total number of taxa expected to occur in five geographical regions located within the Western and Eastern Canadian Arctic biogeographic units (DFO 2009, 2011). From west to east these five regions are: Beaufort Sea, Amundsen Gulf, Western Archipelago, Eastern Archipelago, and Baffin Bay. These five geographical regions also correspond largely to annual discrete sampling segments (legs) of the CCGS *Amundsen* program. Consequently, the present results inform national programs, such as the Fisheries and Oceans Canada (DFO) conservation assessments, and the planning of future field campaigns aiming at increasing megabenthic species records in the Canadian Arctic. This study also increases our knowledge of the marine diversity on a pan-Arctic level and will serve as a benchmark against which changes in megabenthic diversity deriving from species range shifts or invasive species could be identified (e.g.,Węsławski *et al.* 2011).

MATERIALS AND METHODS

Study area

This study was conducted across the Canadian Arctic from the Mackenzie Shelf in the southeastern Beaufort Sea in the west (135°W) to northern Baffin Bay in the east (65°W) (Figure 6). The two main water masses flowing through the Canadian Arctic originate mainly from the Pacific and Atlantic oceans. The colder-fresher Pacific-origin waters (on average < 200 m depth) overlie the warmer-saline Atlantic-origin waters below (on average > 200 m depth) (McLaughlin *et al.* 2004). The transition between these water masses across the study area coincides generally with the 200 m isobath along the shelf break (O'Brien *et al.* 2006; Spalding *et al.* 2007). The Beaufort Sea and Amundsen Gulf regions are highly influenced by the Mackenzie River that drains a watershed of 1.7 x 10^6 km^2 and discharges approximately 340 km^3 y^{-1} of freshwater (McLaughlin *et al.* 2004) and 127 x 10^6 Mt y^{-1} of sediment load (Macdonald *et al.* 2004) into the Beaufort Sea. The complex topography of the Canadian Arctic Archipelago with its numerous islands and channels has a profound influence on sea ice circulation and marine biological productivity regimes (Michel *et al.* 2006). During winter the study area is ice-covered and sea ice could be found throughout the summer as landfast ice or first-year and multiyear pack ice (Howell *et al.* 2009; EC 2010). Summer sea ice distribution along with ice break-up and freeze-up dates exhibit large inter-annual variations (Howell *et al.* 2009; EC 2010). As a general trend, ice in summer remains longer in the central part of the Archipelago than in areas where large and latent heat polynyas open in spring, such as the North Water (NOW), Lancaster Sound-Bylot Island (LS-BI), and the Cape Bathurst (CB) polynyas (Michel *et al.* 2006; Howell *et al.* 2008) (Figure 6). Polynyas located in the northeastern Canadian Arctic (i.e., NOW and LS-BI) exhibit intense marine biological productivity and tight pelagic-benthic coupling as revealed by field observations of diatom-based phytoplankton communities (Ardyna *et al.* 2011), satellite-derived high annual primary production (PP) estimates (Bélanger *et al.* 2013), and high sediment chlorophyll *a* (Chl *a*) concentrations and benthic boundary fluxes (Kenchington *et al.* 2011; Link *et al.* 2013b). In the CB polynya, in contrast, highly variable intensity, timing and duration of phytoplankton blooms (Arrigo & van Dijken 2004), and strong grazing pressure by zooplankton leads to weak pelagic-benthic coupling (Conlan *et al.* 2008; Darnis *et al.* 2012; Link *et al.* 2013b). The central Archipelago has been defined as an oligotrophic system (Ardyna *et al.* 2011).

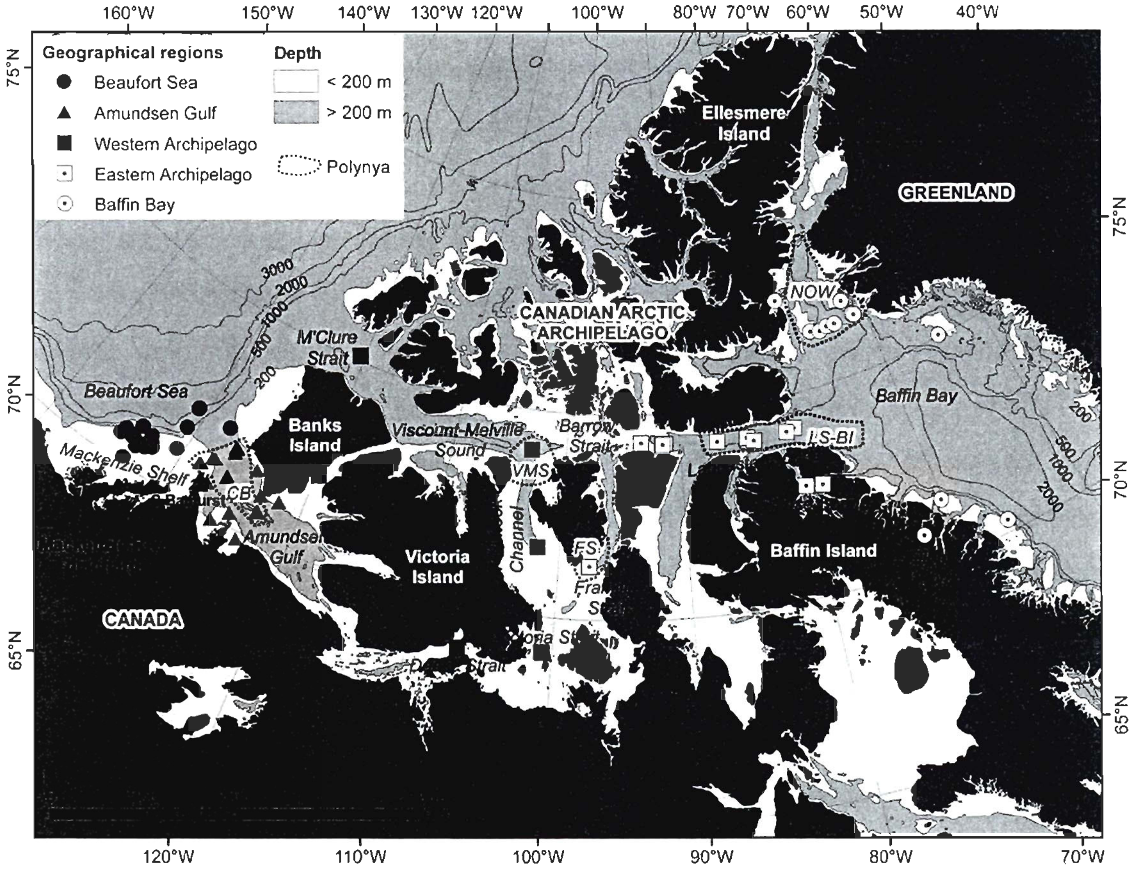


Figure 6. Locations of the 78 stations sampled from 2007-2011 across the Canadian Arctic. Symbols represent five geographical regions within the Western Canadian Arctic biogeographic area (black symbols) and Eastern Canadian Arctic biogeographic area (white symbols) (DFO 2009, 2011). Main polynyas are indicated by dotted polygons and by capital italic letters (*CB*: Cape Bathurst Polynya, *FS*: Franklin Strait Polynya, *LS-BI*: Lancaster Sound-Bylot Island Polynya, *NOW*: North Water Polynya, *VMS*: Viscount-Melville Sound Polynya). Mackenzie River discharge area is indicated by a black arrow. Colder-fresher Pacific-origin water mass is restricted to the upper 200 m (white) with warmer-saline Atlantic-origin water mass underneath (gray).

Faunal data collection

Benthic megafauna were sampled at 78 stations between June and October from 2007 to 2011 onboard the Canadian research icebreaker CCGS *Amundsen* (Figure 6). Station depths ranged from 34 to 1024 m, all below the average ice scouring zone (Gutt 2001; O'Brien *et al.* 2006). All faunal samples were collected with an Agassiz trawl (effective opening of 1.5 m and a 40 mm net mesh size, with a 5 mm cod end liner) with average trawling time and speed of 5 min and 1.5 knots, respectively. In order to standardize community characteristics among stations (by m^2), bottom trawling time and vessel speed at each station were used to calculate towed area (trawl opening of 1.5 m × distance towed; average trawled area of 372 ± 161 m^2). This trawl design is very effective at collecting both epibenthic and burrowing, large-sized invertebrates. Based on the methodology of Piepenburg *et al.* (1996), invertebrates larger than 2 cm were sorted from the trawl catches directly after capture and classified as megabenthos. In addition, the sediment contained in the catches was washed through a 2 mm sieve under running seawater onboard (Piepenburg *et al.* 1996). Planktonic invertebrates that were accidentally taken by the trawl (e.g., Chaetognatha, Euphausiacea, Scyphozoa) and Pisces were removed to only include benthic invertebrates in the sample analysis. Members of the class Ascidiacea were not considered in this study due to exclusion of this taxon during the first years of sampling. Only large echinoderm taxa that could be reliably identified to species level were counted and wet-weighed in the field given the low precision of on-board mass measurements (detection limit of 5 g). All other taxa were preserved in a 4 % seawater-formaldehyde solution buffered with sodium tetraethylborate or frozen for later identification in the lab, and their biomass was determined as formaldehyde wet mass or wet mass (after thawing) at 0.001 g precision. Possible biases in total biomass calculations introduced by different preservation methods were considered minor since all specimens within a phylum were processed the same way and trawl catches were considered semi-quantitative estimates (Eleftheriou & McIntyre 2005; Wetzel *et al.* 2005). Only specimens with the head-part intact were counted and identified to the lowest possible taxonomic level. However, some taxa were left at the phylum level because no complete identification keys exist for Canadian Arctic waters (e.g., Brachiopoda, Nemertea, Platyhelminthes, Porifera); we acknowledge that their richness will have been underestimated in this study. Taxonomic names were verified using the World Register of Marine Species (WoRMS; Appeltans *et al.* 2014). Four species of the phylum Bryozoa and one from the phylum Hydrozoa were not listed in WoRMS but were verified using the Integrated Taxonomic Information System (ITIS, www.itis.gov) (i.e., Bryozoa: *Cellepora smitti, Escharopsis rosacea, Escharopsis sarsi, Porella sacata;* Hydrozoa: *Obelia loveni*).

Data analysis

Megabenthic community characteristics (univariate) and community composition (multivariate) regionally were compared among the five geographical regions from west to east: Beaufort Sea, Amundsen Gulf, Western Archipelago, Eastern Archipelago, and Baffin Bay (Figure 6). Because sampling efforts differed in the five geographical regions, the observed number of taxa was compared to the rarefied number of taxa expected to be documented in each geographical region if only nine stations had been sampled (RS_9, the smallest number of stations observed was in the Western Archipelago) and to non-parametric Chao 2 estimates of predicted number of taxa (Magurran 2004). Station-based rarefaction curves (999 permutations), which are the equivalent of 'randomized' or 'smoothed' species accumulation curves (Gotelli & Colwell 2001), were used to calculate RS_9. Following Whittaker (1972) and Gray (2000) terminology, taxonomic richness in each of the five geographical regions represented γ diversity, and taxonomic richness at a given station was α diversity. The turnover (β) diversity, which relates to the extent of change in species composition among samples along a gradient, was assessed using Whittaker's classical β_W diversity index ($\beta_W = \gamma/\text{mean}(\alpha)$; Whittaker 1972, Magurran 2004). In addition, we used a multivariate measure based on the mean Bray-Curtis dissimilarity (%) between all combinations of stations from a given geographical region (β_{BC}; Magurran 2004). For both β diversity indices higher values represent higher β diversity. Bray-Curtis dissimilarity was calculated on the fourth-root-transformed biomass matrix so that colonial taxa could be included (also see multivariate analyses below).

Regionally mean benthic community characteristics considered in this study for each of the five geographical regions were biomass (g m^{-2}), density (ind. m^{-2}), and four biodiversity metrics (taxonomic richness (number of taxa $station^{-1}$), taxonomic richness density (number of taxa 1000 m^{-2}), Shannon-Wiener's diversity index (H', using $\log_e$), and Pielou's evenness index (J')). H' and J' were calculated based on biomass data including colonial taxa. Density was calculated after removal of colonial taxa because their abundance cannot be recorded (i.e., Bryozoa, Hydrozoa, Nephtheidae (soft corals), Porifera). Analysis of variance (ANOVA) with Tukey post-hoc multiple comparison tests were carried out to test differences in benthic community characteristics among geographical regions. Normality was tested using Shapiro-Wilk's test and homogeneity of variances was determined using Bartlett's test. Data were transformed to satisfy both assumptions when necessary.

For multivariate analyses, lists of taxa at each station were scaled at the genus level and taxa only found at one station were discarded, for a total of 303 taxa found at least at two stations. Singletons in multivariate analysis are prone to random and uninterpretable fluctuations, and it is consequently suggested to remove them to allow better detection of the underlying community similarities (Clarke & Warwick 2001). Scaling at the genus level was done since identifications were patchy at the species level among stations; in some cases specimens were incomplete and missing criteria prevented identification at the species level. Bray-Curtis similarity was calculated for the fourth-root-transformed biomass matrix rather than for the density matrix to be able to include colonial taxa. The fourth-root transformation was chosen to balance the effects of high-biomass taxa and low-biomass taxa, as we were interested in the responses of the whole communities (Clarke & Warwick 2001). Analyses of similarity (ANOSIM) on the biomass-based Bray-Curtis similarity matrix were used to seek differences in community composition among the geographical regions. Similarity Percentages Test (SIMPER) through the Bray-Curtis similarity matrix was used to identify the top 3 taxa contributing most to the dissimilarity between significant regional differences provided by ANOSIM analysis above. SIMPER analysis was also used to identify the top 3 characteristic taxa of the five geographical regions.

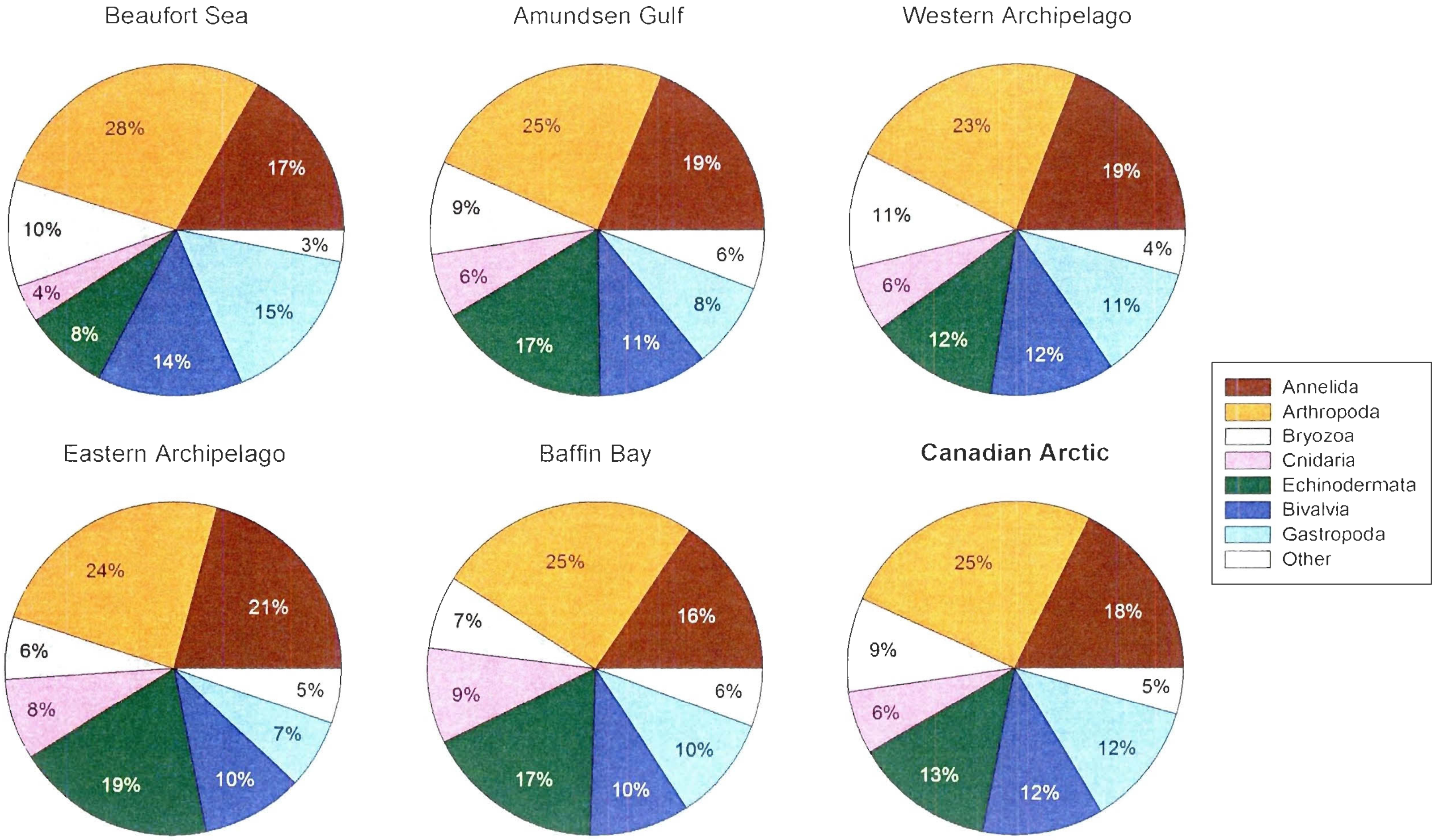
Rarefaction curves, Chao 2 estimates, MDS, ANOSIM and SIMPER analyses were performed using PRIMER-E software version 6 (Clarke & Gorley 2006). All other tests were performed using the statistical package R version 3.0 (R Core Team 2013). Statistical significance at $\alpha < 0.05$ was used for all statistical tests except for post-hoc multiple comparison tests (ANOVA, ANOSIM) where a statistical significance at $\alpha < 0.01$ was used to account for the increasing probability of type I error in multiple testing (Quinn & Keough 2002).

RESULTS

Faunal inventory

A total of 527 taxa were identified at the lowest possible taxonomic level across 13 phyla (430 at the species level) (Appendix 1). Arthropoda occurred with the highest number of taxa (n = 161; mostly Crustacea), followed by Annelida (n = 122; mostly Polychaeta), Mollusca (n = 114; mostly Bivalvia and Gastropoda), Bryozoa (n = 50), Echinodermata (n = 43), Cnidaria (n = 27; Anthozoa and Hydrozoa), and other phyla with one to three taxa (Brachiopoda, Cephalorhyncha, Entoprocta, Nemertea, Platyhelminthes, Porifera, Sipuncula). Arthropoda and Annelida represented on average 25 % and 18 %, respectively, of all megabenthic taxa across the Canadian Arctic (Figure 7), while Echinodermata represented on average 44 % of the biomass (Figure 8). Across the Canadian Arctic, the five most common taxa were the ophiuroids *Ophiocten sericeum* (found at 55 % of stations), *Ophiacantha bidentata* (48 %) and *Ophiopleura borealis* (33 %), the soft corals Nephtheidae (48 %), and the onuphid polychaete *Nothria conchylega* (39 %).

Observed regional taxonomic richness (S_{obs}), or γ diversity, was higher in the Beaufort Sea and Amundsen Gulf regions, where sampling effort was highest, than in Western and Eastern Archipelago regions and in Baffin Bay (Table 1, Figure 9). Rarefied number of taxa expected for each geographical region (RS_9) was highest in the Western Archipelago region and lowest in the Amundsen Gulf region (Figures 9 and 10). Station-based rarefaction curves for each of the five geographical regions did not reach a plateau (Figure 10). Chao 2 estimates were highest for the Amundsen Gulf and the two Archipelago regions, followed by the Beaufort Sea and Baffin Bay regions (Table 1, Figure 9). Between 41 % and 50 % of expected taxa were documented in the Amundsen Gulf and the two Archipelago regions, while almost 60 % and 70 % of expected taxa were documented in Baffin Bay and the Beaufort Sea regions, respectively (Table 1). Turnover (β) diversity was relatively similar in all regions, but considerably higher in the Amundsen Gulf region, where both β_w and β_{BC} were the highest (Figure 9).



Beaufort Sea

Amundsen Gulf

Western Archipelago

Eastern Archipelago

Baffin Bay

Canadian Arctic

Figure 7. Variation in mean relative taxonomic richness (%) for the main phyla or class sampled in the five geographical regions and for the Canadian Arctic as a whole.

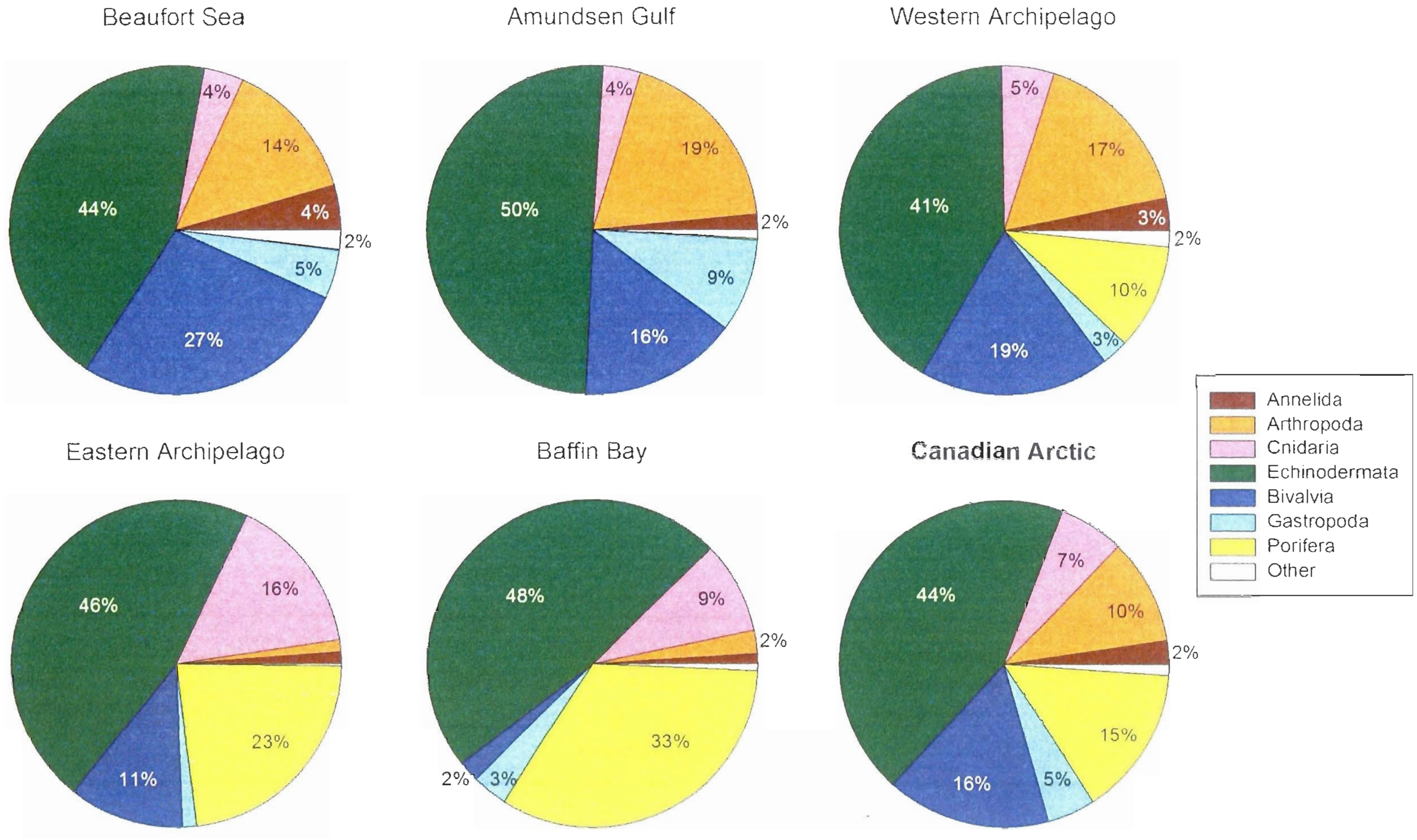


Figure 8. Variation in relative mean biomass (%; only ≥ 2 % shown) for the main phyla or class sampled in the five geographical regions and for the Canadian Arctic as a whole.

Table 1. Richness estimates and turnover (β) diversity for the five geographical regions. Rarefied number of taxa expected to be documented in each geographical region based on nine stations (RS_9; based on the least sampled region, i.e., the Western Archipelago), observed number of taxa (S_{obs} or regional (γ) diversity), Chao 2 estimates of predicted number of taxa, as well as the predicted proportion of documented (S_{obs} /Chao 2) and undocumented taxa (100 - % documented taxa). β diversity indices using Whittaker's index (β_W; based on number of taxa) and mean Bray-Curtis dissimilarity (β_{BC}; based on distribution of biomass among the taxa).

			Number of taxa					Turnover (β) diversity	
Geographical region	No. of stations	Depth (m; mean ± SD)	RS_9 (mean ± SD)	S_{obs} or γ diversity	Chao 2 estimate (mean ± SD)	Predicted proportion of documented taxa (%)	Predicted proportion of undocumented taxa (%)	β_W	β_{BC}
Beaufort Sea	20	153 ± 240	234 ± 17	335	507 ± 39	66	34	5.9	79.1
Amundsen Gulf	23	257 ± 181	164 ± 27	300	599 ± 63	50	50	10.9	86.4
Western Archipelago	9	166 ± 137	255	255	556 ± 69	46	54	5.0	82.5
Eastern Archipelago	13	438 ± 258	198 ± 13	250	617 ± 88	41	59	6.6	78.5
Baffin Bay	13	497 ± 164	196 ± 18	243	416 ± 40	58	42	6.5	82.2

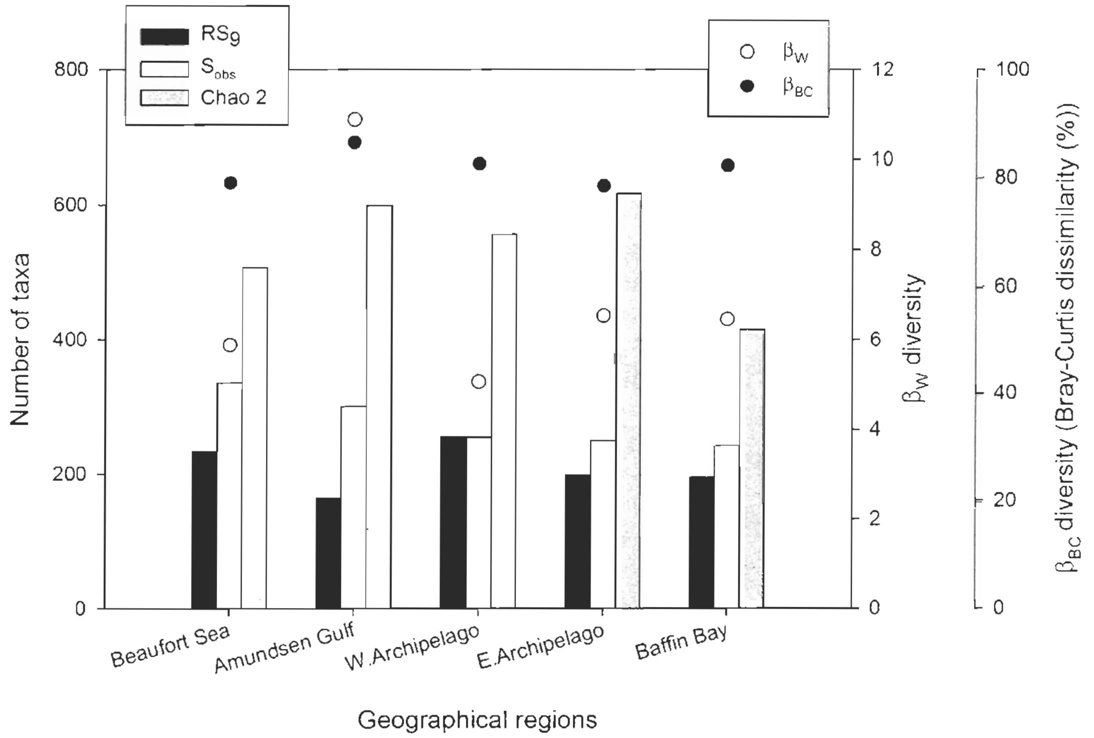


Figure 9. Richness and turnover (β) diversity in the five geographical regions. Rarefied number of taxa expected to be documented in each geographical region based on nine stations (RS_9), observed number of taxa (S_{obs} or regional (γ) diversity), as well as Chao 2 estimates of predicted number of taxa, and β diversity using Whittaker's index (β_W; white circles) and mean Bray-Curtis dissimilarity (β_{BC}; black circles). E: Eastern, W: Western.

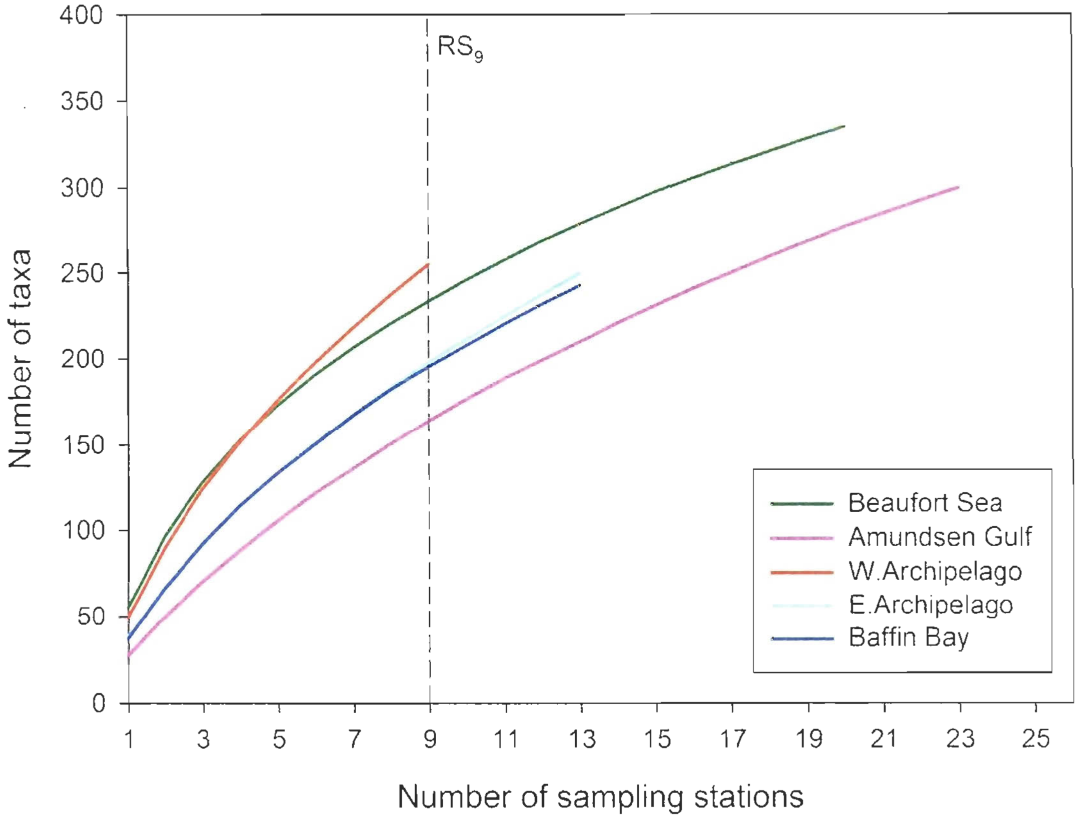


Figure 10. Station-based rarefaction curves for the five geographical regions. RS$_9$ represents the rarefied number of taxa expected to be documented in each geographical region based on nine stations (999 permutations). E: Eastern, W: Western.

Regional comparisons

Relative taxonomic richness of the main phyla did not vary greatly between the geographical regions (Figure 7). However, mean relative biomass of the main phyla varied among the geographical regions (Figure 8). The biomass proportions of Arthropoda, Bivalvia and Gastropoda were greatest in the Western Canadian Arctic regions (Beaufort Sea, Amundsen Gulf, Western Archipelago) compared with in the Eastern Canadian Arctic regions (Eastern Archipelago, Baffin Bay) (Figure 8). Cnidaria and Porifera were proportionally greatest, in terms of biomass, in the Eastern Canadian Arctic regions (Eastern Archipelago, Baffin Bay) (Figure 8). Among the benthic community characteristics tested, only richness and richness density were significantly lower in the Amundsen Gulf region than in the neighboring Beaufort Sea region (Table 2, Figure 11).

Table 2. Regional comparisons of benthic univariate community characteristics (ANOVA analysis) and of multivariate (biomass-based) community composition (ANOSIM analysis). E: Eastern, W: Western; ns: non-significant.

Community characteristic	Geographical regions (significant differences are shown if $p < 0.01$)
Univariate	
ln(biomass)	ns
ln(richness)	Amundsen Gulf < Beaufort Sea
ln(richness density)	Amundsen Gulf < Beaufort Sea
ln(density)	ns
H’	ns
J’	ns
Multivariate	
Community composition (4th-root transformed)	Global test (R=0.229) Beaufort Sea *vs.* Amundsen Gulf (R=0.252) Beaufort Sea *vs.* W. Archipelago (R=0.299) Beaufort Sea *vs.* E. Archipelago (R=0.445) Beaufort Sea *vs.* Baffin Bay (R=0.495) W. Archipelago *vs.* Baffin Bay (R=0.317)

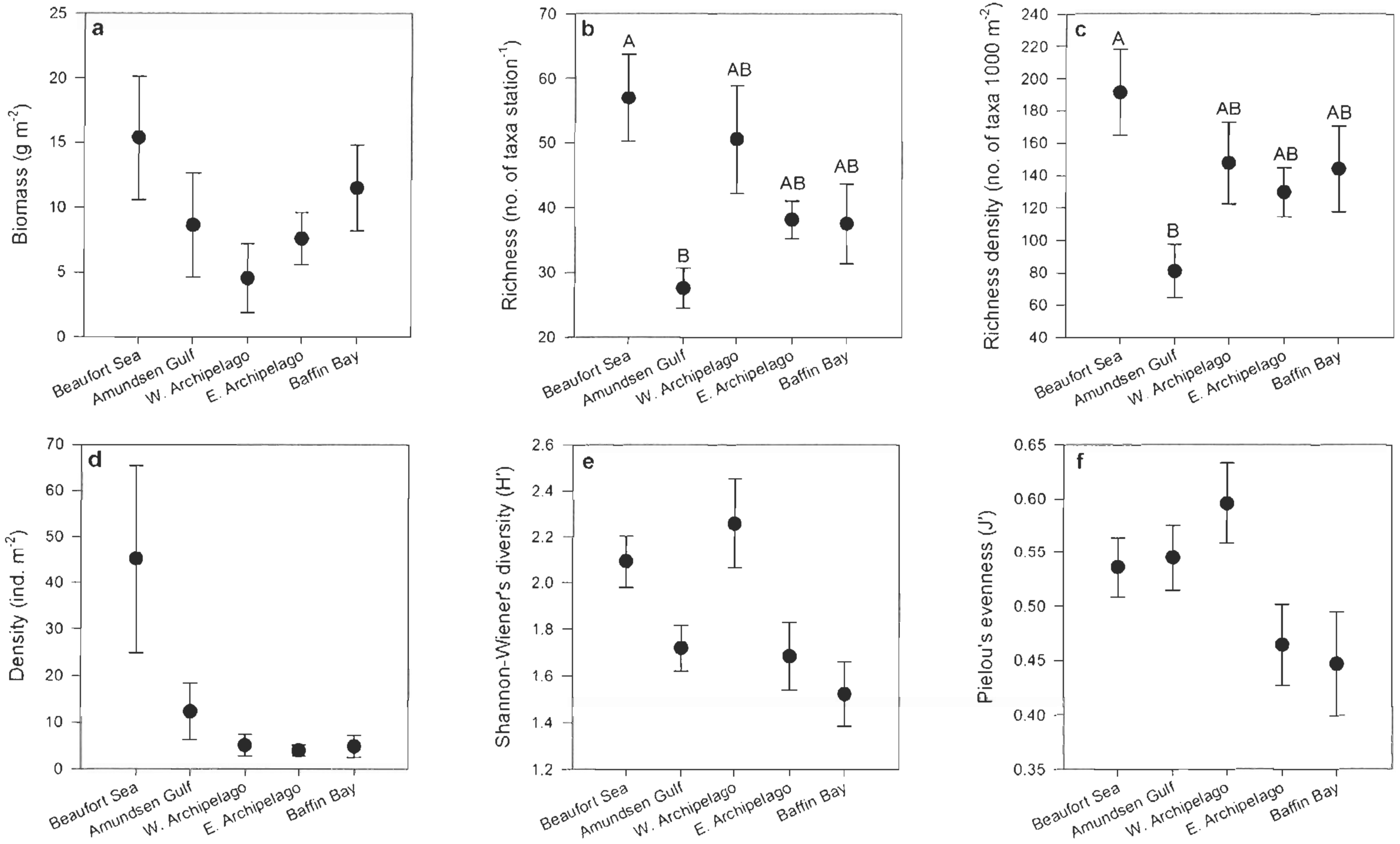


Figure 11. Mean (± SE) benthic community characteristics for the five geographical regions. (**a**) biomass (g m^{-2}); (**b**) richness (no. of taxa $station^{-1}$); (**c**) richness density (no. of taxa 1000 m^{-2}); (**d**) density (ind. m^{-2}); (**e**) Shannon-Wiener's diversity index (H'); (**f**) Pielou's evenness index (J'). Different letters (A, B) above points indicate significant differences ($p < 0.01$) based on ANOVA tests (after data transformation; see Table 2). E: Eastern, W: Western.

Megabenthic community composition was not strongly different among geographical regions with poor segregation of the geographical regions in the MDS (relatively high stress level, > 0.2), except for a greater separation of the Beaufort Sea region (Figure 12). ANOSIM analysis revealed that community composition of the Beaufort Sea region was significantly different than in all other regions, and that community composition in the Western Archipelago was different than in Baffin Bay (Table 2). However, ANOSIM R' values overall were small (R < 0.5). SIMPER analysis on those regions that significantly differ in community composition as determined by ANOSIM analysis showed between region dissimilarity to be high on average (84 %), varying from 82 % to 87 % (Table 3). Among the top 3 megabenthic taxa contributing most to dissimilarity between each of the significant regional differences, the isopod *Saduria* spp. always appeared as a significant discriminant taxon between the Beaufort Sea region and the other four regions (Table 3). The cumulative percentage of dissimilarity explained by the top 3 megabenthic taxa was on average low (7.5 %), since up to 82 taxa were needed on average to reach a cumulative percentage of dissimilarity of 75 % (list of these taxa not shown). SIMPER analysis showed within-region similarity to be low on average (23 %), varying from 18 % to 28 % (Table 4). Some of the top 3 characteristic taxa of within-region similarity were found in more than one geographical region (e.g., the bivalve *Astarte* spp. and the ophiuroids *Ophiacantha* sp., *Ophiocten* sp. and *Ophiopleura* sp.) (Table 4). The bivalve *Macoma* spp. was a characteristic taxon of the Beaufort Sea region, while the soft corals Nephtheidae were a characteristic taxon of the Eastern Archipelago region (Table 4).

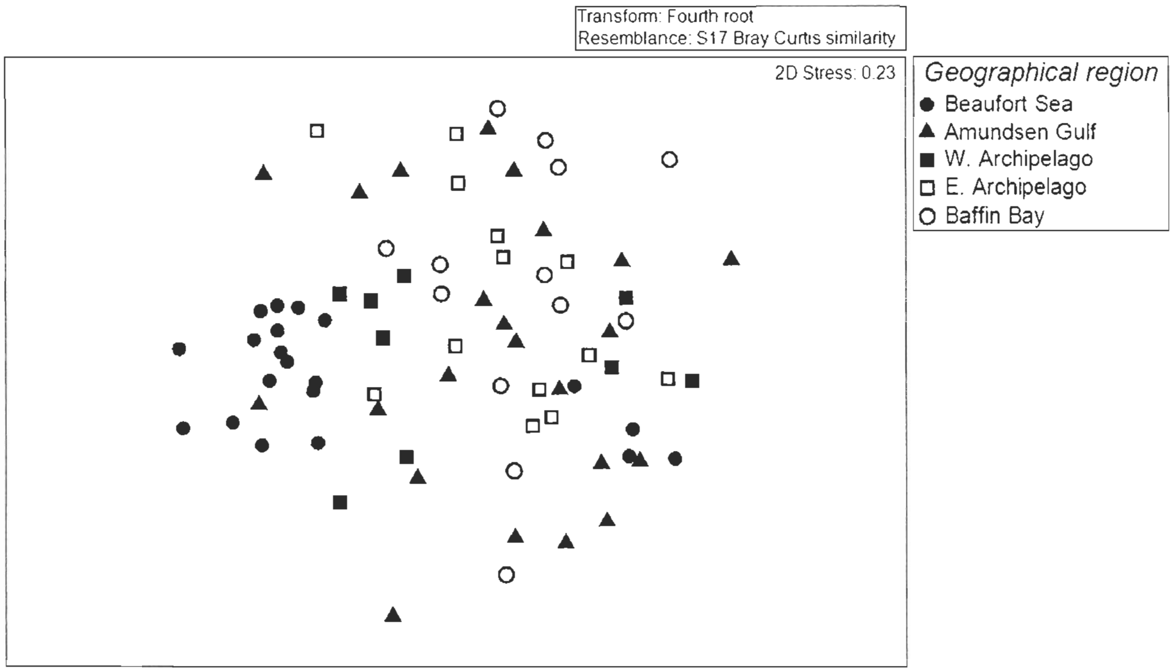


Figure 12. Non-metric multidimensional scaling (MDS) ordination of megabenthic community composition of the five geographical regions. Based on Bray-Curtis similarity biomass-based matrix after fourth-root transformation. E: Eastern, W: Western.

Table 3. Top 3 megabenthic taxa contributing most to dissimilarity between those regions that significantly differ in community composition based on biomass, as determined by ANOSIM analysis in Table 2. Contrib.: percent contribution, Cum.: percent cumulative; E: Eastern, W: Western.

Regional comparison/Taxon	Average biomass		Average dissimilarity	SD of dissimilarity	Contrib.	Cum.
	(g m^{-2})		(%)	(%)	(%)	(%)
Beaufort Sea *vs.* Amundsen Gulf; average dissimilarity = 85 %	Beaufort Sea	Amundsen Gulf				
Saduria spp.	1.57	0.06	2.42	1.40	2.86	2.86
Astarte spp.	1.96	0.20	1.93	1.19	2.28	5.14
Icasterias sp.	2.10	0.05	1.90	1.04	2.25	7.39
Beaufort Sea *vs.* W. Archipelago; average dissimilarity = 82 %	Beaufort Sea	W. Archipelago				
Saduria spp.	1.57	0.07	2.12	1.28	2.59	2.59
Ophiocten sp.	1.30	0.38	1.69	1.43	2.06	4.64
Astarte spp.	1.96	0.13	1.57	1.13	1.91	6.56
Beaufort Sea *vs.* E. Archipelago; average dissimilarity = 85 %	Beaufort Sea	E. Archipelago				
Saduria spp.	1.57	0	2.27	1.53	2.67	2.67
Gorgonocephalus sp.	1.55	2.66	2.18	0.77	2.55	5.22
Astarte spp.	1.96	0.48	1.89	1.22	2.22	7.44
Beaufort Sea *vs.* Baffin Bay; average dissimilarity = 87 %	Beaufort Sea	Baffin Bay				
Ophiura sp.	0.31	0.62	2.35	1.37	2.70	2.70
Saduria spp.	1.57	0	2.29	1.42	2.62	5.32
Ophiopleura sp.	0.09	1.64	2.25	0.87	2.59	7.91
W. Archipelago *vs.* Baffin Bay; average dissimilarity = 83 %	W. Archipelago	Baffin Bay				
Ophiura sp.	< 0.01	0.62	2.66	1.38	3.18	3.18
Ophiopleura sp.	0.06	1.64	2.54	0.94	3.05	6.23
Ophiacantha sp.	0.28	0.13	1.67	1.28	2.00	8.23

Table 4. Top 3 megabenthic characteristic taxa contributing most to similarity within each of the five geographical regions. Contrib.: percent contribution, Cum.: percent cumulative; E: Eastern, W: Western.

Region/Taxon	Average biomass (g m^{-2})	Average similarity (%)	SD of similarity (%)	Contrib. (%)	Cum. (%)
Beaufort Sea; average similarity = 28 %					
Saduria spp.	1.57	2.22	1.13	7.99	7.99
Ophiocten sp.	1.30	1.21	0.89	4.34	12.33
Macoma spp.	0.30	1.19	0.91	4.27	16.61
Amundsen Gulf; average similarity = 18 %					
Ophiocten sp.	0.16	2.05	0.98	11.30	11.30
Astarte spp.	0.20	1.90	0.76	10.46	21.76
Ophiacantha sp.	0.13	1.81	0.80	9.96	31.72
W. Archipelago; average similarity = 22 %					
Ophiacantha sp.	0.28	2.86	1.35	13.24	13.24
Ophiocten sp.	0.38	2.02	1.00	9.36	22.60
Astarte spp.	0.13	1.28	0.70	5.89	28.49
E. Archipelago; average similarity = 26 %					
Nephtheidae	0.44	2.30	1.32	8.93	8.93
Ophiopleura sp.	0.21	1.99	0.87	7.72	16.65
Astarte spp.	0.48	1.73	0.67	6.73	23.38
Baffin Bay; average similarity = 22 %					
Ophiura sp.	0.62	3.35	1.23	14.90	14.90
Ophiopleura sp.	1.64	1.76	0.52	7.81	22.71
Astarte spp.	0.21	1.58	0.75	7.02	29.73

DISCUSSION

This study reports comparisons of megabenthic richness across five geographical regions of the Canadian Arctic. We compare predicted regional richness estimates with other Arctic regions and we discuss the methodological constraints that hamper comparisons of observed richness among Arctic megabenthic studies. Our results show overall high similarity in megabenthic community characteristics among the study regions with significant differences only observed between the Beaufort Sea and Amundsen Gulf regions. In terms of community composition, the Beaufort Sea region was significantly dissimilar to all other geographical regions.

High richness across the Canadian Arctic

The overall high observed richness for all geographical regions in this study provides an important advancement in our understanding of marine diversity in the Canadian Arctic, a severely undersampled region of the Arctic Ocean (Archambault *et al.* 2010; Piepenburg *et al.* 2011). None of the species accumulation curves reached a plateau, and in fact, only about 40 % to 70 % of predicted taxa per region were documented, indicating that about a third to a half of the expected species pool is still unrecorded. Predicted richness estimates for the study regions are in the range of estimates (using Chao 2 estimator) predicted for other Canadian Arctic regions, such as Northern Labrador (591 taxa) and Hudson Bay Complex (483 taxa), and for other Arctic shelves in close proximity to the Canadian Arctic, such as West and North Greenland (432-478 taxa) and the Chukchi Sea (443 taxa) (Piepenburg *et al.* 2011). Lower and higher predicted richness estimates have been documented for the Siberian seas (161-311 taxa) and the Barents Sea (712 taxa), respectively (Piepenburg *et al.* 2011). The occurrence of large rivers draining into the Siberian seas likely explain the lower richness of these Arctic shelves, but the pronounced differences in sampling effort among regions may also generate these dissimilarities (Piepenburg *et al.* 2011). For instance, the Barents Sea is one of the most thoroughly studied Arctic regions, possibly coincident with the high species records.

As opposed to comparison of predicted richness estimates, comparison of observed richness estimates among Arctic megabenthos studies are hampered by methodological constraints. First, the few Arctic studies that have used trawl for sampling megafauna have employed different types of trawl (Piepenburg *et al.* 1996; Feder *et al.* 2005; Bluhm *et al.* 2009; Ravelo *et al.* 2013), this study), which are known to differ in their sediment penetration and ability to catch some large infaunal specimens (Eleftheriou & McIntyre 2005). In addition, studies using trawls do not generally cover the same depth range and geographic extent, hindering direct comparisons of absolute species numbers. Lastly, most of Arctic megabenthic research used videos and images, thus producing generally less in-depth taxonomic determination (e.g., Piepenburg & Schmid 1997; Bluhm *et al.* 2005; Soltwedel *et al.* 2009). Regardless, additional sampling in the Canadian Arctic, and the Arctic in general, will certainly improve the pan-Arctic assessment on megabenthic richness, but there is growing evidence that nearly all Arctic shelf regions host rich and diverse benthic communities (Piepenburg *et al.* 2011).

Three out of the five most widely distributed taxa in the present study area, the brittle stars (ophiuroids) *Ophiocten sericeum* and *Ophiacantha bidentata* and the onuphid polychaete *Nothria conchylega* are common throughout the Arctic shelves (Piepenburg *et al.* 2011). The strong circumpolar presence of ophiuroids in many shelf and slope habitats is a general pattern in Arctic epibenthic community composition, presumably because predation pressure on these taxa is low (Piepenburg 2000). The high respiration rates of ophiuroids make them important ecological players in carbon remineralization on Arctic shelves, although their importance is often neglected in carbon cycling models (Ambrose *et al.* 2001). The broad diet spectrum of ophiuroids (commonly surface deposit feeders and omnivorous; Piepenburg 2000) and of onuphids (predator/scavenger; Fauchald and Jumars 1979) may support their widespread occurrence.

Regional comparisons

Highest β diversity was observed in the Amundsen Gulf, reflecting high habitat heterogeneity in the region. The Amundsen Gulf region is composed of a narrow shelf subjected to intense erosion, a steep continental slope, and is influenced to the west by the Mackenzie River sediment load discharge and a strong upwelling current near Cape Bathurst (O'Brien *et al.* 2006; Williams & Carmack 2008). While having high habitat heterogeneity, this region had significantly lower mean richness than the Beaufort Sea region. The higher number of stations sampled at great water depths in the central Amundsen Gulf region than in the Beaufort Sea region may be an important factor explaining this difference in richness based on the typically lower species richness at depth (Levin *et al.* 2001). Besides richness, the geographical regions did not differ significantly in their mean benthic community characteristics and revealed overall high diversity similarity among regions. Contrary to our results, Cusson *et al.* (2007) reported from historical macrobenthic data from the 1950's to 1970's that the Beaufort Sea region had moderate species richness and low H' diversity compared to eastern regions of the Canadian Arctic. Our study did not include nearshore stations that are often under severe seasonal disturbances, such as variable salinity and ice scouring, which were suggested to drive some of the observed difference in macrofaunal diversity patterns (Cusson *et al.* 2007). The distinctiveness of the Beaufort Sea region was rather revealed in our study on megafauna by the slightly different community composition of this region with all the other regions. For instance, the isopod *Saduria* spp. is euryhaline (Percy 1983; Hagerman & Szaniawska 1988) and its high average biomass in the Beaufort Sea region compared with the other regions presumably reflected the strong influence of the Mackenzie River on the Beaufort Sea community composition.

The overall high similarity among geographical regions, both in terms of community characteristics and community composition, reflects the weak effect of regional divisions on benthic patterns. Across the study area, Roy *et al.* (2014) have defined six megabenthic communities, according to their biomass-based community composition. Community patterns were spatially organised according to large-scale environmental gradients (e.g., depth and water masses) and meso-scale gradients (e.g., substrate type, food supply proxies). Except for one community spatially restricted on the Mackenzie Shelf in the Beaufort Sea region, all the other communities were found in more than one of the regions considered in the present study. The widespread occurrence of many of the megabenthic communities defined by Roy *et al.* (2014) across the Canadian Arctic is likely explained by the fact that each of the geographical regions covered similar depth gradients and contained distinct water masses (Pacific vs. Atlantic) and substrate (hard vs. soft) gradients, which are more important in driving benthic spatial patterns than are geographical divisions. Benthic geographical differences are only well-defined in regions that have specific environmental conditions, such as in the western Canadian Arctic regions (Beaufort Sea and Amundsen Gulf regions) where the Mackenzie River has a profound influence on the oceanographic setting. The high terrestrial carbon and freshwater influxes from the Mackenzie River (Carmack & MacDonald 2002; Macdonald *et al.* 2004) exert a particular environmental forcing on benthos in these western regions, especially on the shelf (Conlan *et al.* 2008; Conlan *et al.* 2013). Additionally to current environmental conditions driven by the Mackenzie River attributes, geological events during the Pleistocene have shaped the evolutionary history of benthic spatial patterns in the Canadian Arctic by reducing faunistic interchange during glaciation between the north Atlantic and Pacific (Lubinsky 1972). Based on these results, any assessment- and/or management-based approaches that consider benthic spatial variability across the Canadian Arctic regions should focus primarily on the influence of environmental gradients on benthic patterns and less on the weak influence of geographical divisions.

CONCLUSION

Marine ecosystems of the Arctic will experience numerous changes with the expected loss of summer sea ice in the near future (Post *et al.* 2013). Extensive baseline data documenting present ecosystem condition (e.g., biodiversity) are crucial to monitor and predict impacts of climate changes on these ecosystems. This study and subsequent efforts across the Canadian Arctic contribute to pan-Arctic initiatives, such as the Circumpolar Biodiversity Monitoring Program (CBMP; Gill *et al.* 2011), that harmonize and integrate efforts to globally monitor Arctic marine biota and the effects of climate change. Recent research initiatives have considerably increased our understanding of Arctic marine biodiversity (e.g., Bluhm *et al.* 2011b), but few Arctic studies have attempted to study megabenthic diversity across continental scales. The present study provides a significant advancement for our assessment of marine diversity in the Canadian Arctic, and a baseline for future comparisons. However, while we demonstrated that observed megabenthic richness was relatively high in all regions, future sampling is needed to increase actual species records across the Canadian Arctic. This is especially important in the Western and Eastern Archipelago regions where we estimated that 54 % and 59 % of taxa, respectively, still have to be documented. In addition, the overall weak influence of geographic divisions on megabenthic community patterns in this study strongly suggest to focus on environmental forcing when interpreting benthic spatial patterns across the Canadian Arctic.

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Appendix 1.

Faunal inventory of all megabenthic taxa identified at the lowest possible taxonomic level across five geographical regions of the Canadian Arctic. Taxa are ordered alphabetically within each phylum and class. Taxonomic identifications were conducted by the first author (Virginie Roy) and by specialists at the Benthic Ecology Lab (Bernard Boucher, Laure de Montety and Lisa Tréau de Coeli; *Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, QC, Canada*). After identification, specimens were transferred to 70 % isopropanol for long-term storage.

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Annelida	**X**	**X**	**X**	**X**	**X**
Clitellata		**X**	**X**	**X**	**X**
Calliobdella sp.		X			
Hirudinea			X	X	
Oligochaeta				X	X
Polychaeta	**X**	**X**	**X**	**X**	**X**
Abyssoninoe abyssorum				X	
Abyssoninoe scopa		X			
Abyssoninoe sp.		X			
Aglaophamus malmgreni	X	X	X	X	X
Aglaophamus sp.		X			X
Amage auricula	X	X		X	
Amage sp.		X			
Ampharete acutifrons		X		X	
Ampharete finmarchica		X	X	X	
Ampharete goesi	X				
Ampharete sp.	X	X		X	X
Ampharetidae			X		
Amphicteis gunneri	X	X		X	X
Amphicteis ninonae		X		X	X
Amphicteis sp.		X			
Amphitrite cirrata		X			
Aphelochaeta sp.		X			X
Aphrodita aculeata				X	

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Apomatus globifer	X				
Apomatus similis			X		
Asychis biceps				X	X
Asychis sp.				X	X
Axionice flexuosa	X				
Axionice maculata	X	X	X	X	X
Axionice sp.	X				
Brada inhabilis			X	X	X
Brada villosa	X			X	
Branchiomma sp.	X	X	X		X
Bylgides elegans	X				
Bylgides groenlandicus			X		X
Bylgides sarsi	X				
Bylgides sp.	X	X	X		X
Chaetopteridae		X			
Chaetozone sp.	X		X		X
Chone duneri		X			
Chone gracilis	X				
Chone infundibuliformis	X	X	X		
Chone sp.	X		X	X	
Chone sp./*Jasmineira* sp.	X				
Cirratulidae	X		X		
Cirratulus cirratus			X		
Cirratulus sp.	X		X		
Cistenides hyperborea	X	X		X	X
Cistenides sp.	X	X			
Cryptosclerocheilus baffinensis			X		
Diplocirrus sp.	X			X	
Dipolydora socialis	X				
Ephesiella sp.			X		
Eteone flava/longa	X		X	X	
Euchone analis	X				
Euchone elegans		X			

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Euchone papillosa	X	X	X	X	
Euchone sp.		X			
Eucranta sp.			X		X
Eucranta villosa		X		X	
Eunereis longissima			X		
Eunoe nodosa	X	X	X	X	X
Eunoe oerstedi	X		X		
Euphrosine borealis				X	
Eupolymnia sp.			X		
Fabriciidae			X		
Flabelligera affinis			X		
Flabelligera sp.			X		
Flabelligeridae		X	X		
Galathowenia oculata	X	X			
Gattyana cirrhosa	X	X	X		
Gattyana sp.	X				
Glycera capitata				X	X
Glyphanostomum pallescens		X	X	X	X
Grubianella klugei	X				
Harmothoe extenuata		X			
Harmothoe rarispina	X				
Harmothoe sp.	X		X	X	
Heteromastus sp.		X			
Jasmineira sp.	X	X	X	X	
Laonice cirrata		X	X	X	X
Laonice sp.		X			
Laonome sp.	X		X		
Leaena abranchiata				X	X
Leaena sp.	X				
Levinsenia gracilis				X	
Lumbrineris fragilis			X	X	X
Lumbrineris impatiens	X	X		X	X
Lumbrineris latreilli	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Lumbrineris scopa				X	
Lumbrineris sp.	X	X		X	
Lysippe labiata	X				
Macellicephala sp.					X
Macellicephala violacea					X
Macellicephalinae		X			
Maldane arctica	X	X		X	
Maldane arctica/sarsi			X	X	
Maldane sarsi	X	X	X		
Maldane sp.	X	X			
Melinna cristata		X		X	
Melinna palmata		X			
Melinna sp.			X		
Melinnexis annenkovae	X				
Melinnopsis arctica	X	X			
Monticellina sp.		X			
Myriochele heeri	X	X	X	X	X
Myriochele olgae	X	X			
Myriochele sp.			X		
Myrioglobula malmgreni	X	X			
Neoamphitrite sp.		X			
Nephtys ciliata	X	X	X	X	X
Nephtys incisa			X	X	
Nephtys longosetosa			X		
Nephtys paradoxa			X		X
Nereididae					X
Nereis sp.	X	X		X	
Nereis zonata	X	X	X	X	X
Nicomache lumbricalis				X	
Nicomache sp.			X	X	X
Nothria conchylega	X	X	X	X	X
Notomastus sp.		X	X		X
Onuphidae			X		

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Ophelina aulogaster		X			
Ophelina cylindricaudata			X		
Oriopsis sp.			X		
Owenia borealis	X	X		X	X
Owenia fusiformis	X	X		X	
Owenia polaris	X	X		X	X
Oweniidae		X			
Paradiopatra quadricuspis		X			
Paramphitrite tetrabranchia		X			
Paranaitis sp.		X	X		
Paranaitis wahlbergi			X		
Paraonis gracilis	X				
Paraonis sp.		X			
Pectinariidae	X				
Petaloproctus tenuis					X
Pholoe sp.		X			
Phyllodoce (Anaitides) groenlandica	X	X	X	X	
Phyllodoce mucosa				X	
Phyllodocidae	X				
Pista elongata					X
Polycirrus sp.					X
Polynoidae					X
Polyphysia crassa					X
Potamilla neglecta				X	
Prionospio cirrifera		X			
Prionospio sp.				X	
Prionospio steenstrupi	X	X			
Protis arctica	X				
Protula tubularia					X
Pterolysippe vanelli			X		
Sabellidae				X	
Sabellides borealis	X	X		X	
Sabellides octocirrata			X		

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Sabellinae	X				
Samythella neglecta			X		
Scalibregma inflatum	X	X			
Scalibregmatidae					X
Scoletoma tetraura	X				
Scoloplos armiger	X				X
Scoloplos sp.				X	
Sphaerodoridae	X				
Sphaerodorum sp.				X	
Spio sp.			X	X	
Spirorbis sp.					X
Terebellides stroemii	X	X	X	X	
Terebellides williamsae	X	X			
Terebellinae				X	
Tharyx sp./*Chaetozone* sp.	X				
Thelepodinae				X	
Thelepus cincinnatus		X	X	X	X
Arthropoda	**X**	**X**	**X**	**X**	**X**
Malacostraca	**X**	**X**	**X**	**X**	**X**
Acanthonotozoma inflatum	X		X	X	
Acanthonotozoma serratum	X				
Acanthostepheia malmgreni	X	X	X		X
Acanthostepheia sp.		X			
Aceroides latipes	X				
Aeginina longicornis				X	X
Amathillopsis spinigera		X	X		
Amblyops sp.				X	
Ampelisca eschrichtii	X	X	X	X	X
Ampelisca macrocephala	X	X	X	X	
Ampelisca sp.	X	X		X	
Anonyx compactus				X	
Anonyx debruyni	X			X	X
Anonyx laticoxae	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Anonyx lilljeborgii					X
Anonyx nugax	X	X	X	X	X
Anonyx pacificus	X		X		
Anonyx sp.	X	X			
Apherusa sp.	X	X			
Arctolembos arcticus	X	X			
Arcturidae				X	
Arcturus baffini				X	X
Arcturus baffini tuberosus			X		
Argis dentata	X	X	X		
Argis sp.	X				
Aristias tumidus					X
Arrhis phyllonyx	X	X	X	X	X
Arrhis sp.	X	X			
Atylus carinatus	X				
Atylus smittii		X			
Birsteiniamysis inermis	X				
Boeckosimus brevicaudatus				X	
Boeckosimus edwardsi			X		
Boeckosimus sp.				X	
Boreomysis arctica	X	X		X	X
Boreomysis sp.	X	X		X	
Byblis erythrops			X		
Byblis gaimardii	X	X	X	X	X
Byblis sp.	X			X	
Bythocaris gracilis/payeri				X	X
Bythocaris sp.	X	X	X		
Caecognathia elongata			X		
Caecognathia stygia		X	X		
Calathura brachiata	X	X	X		
Calliopiidae		X			
Caprella linearis	X				
Centromedon calcaratus		X			

Phylum Class Taxon	Beaufort Sea	Amundsen Gulf	Western Archipelago	Eastern Archipelago	Baffin Bay
Cumacea		X			
Diastylis echinata				X	
Diastylis glabra	X			X	
Diastylis goodsiri	X	X	X	X	X
Diastylis oxyrhyncha	X				
Diastylis rathkei	X	X	X	X	X
Diastylis scorpioides		X	X		
Diastylis sp.		X			
Diastylis spinulosa	X	X	X	X	X
Diastyloides sp.	X				
Epimeria loricata	X	X	X	X	X
Ericthonius punctatus	X				
Ericthonius sp.	X				
Erythrops abyssorum			X		
Erythrops glacialis					X
Eualus fabricii	X				
Eualus gaimardii	X				
Eualus gaimardii belcheri	X		X	X	X
Eualus gaimardii gaimardii	X	X	X	X	X
Eualus sp.	X				
Eudorella emarginata		X			
Eudorella sp.	X				
Eumalacostraca		X			
Eurycope sp.		X			
Eusirus cuspidatus				X	
Eusirus holmi		X			X
Eusirus leptocarpus		X			
Gammaridae			X		
Gnathia sp.	X	X			
Halice abyssi					X
Halirages fulvocinctus		X	X		
Halirages qvadridentatus	X			X	X
Halirages sp.					X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Haliragoides inermis				X	
Haploops laevis	X	X	X		
Haploops sp.	X			X	
Haploops tubicola	X	X	X	X	
Hemiarthrus abdominalis	X				
Hippomedon propinquus				X	
Hyas alutaceus		X			
Hyas sp.			X		
Hymenodora glacialis				X	
Hymenodora sp.	X				
Hyperia galba		X			X
Hyperia spinigera				X	
Ichnopus spinicornis	X				
Ischyroceridae					X
Ischyrocerus latipes	X	X			
Ischyrocerus megacheir				X	
Jassa sp.	X				
Lebbeus polaris	X	X	X	X	X
Lepidepecreella sp.					X
Lepidepecreum serratum					X
Lepidepecreum umbo	X	X	X		
Leucon (Leucon) nasica	X				
Leucon (Leucon) nasicoides	X				
Leucon (Leucon) nathorsti	X				
Leuconidae					X
Lophogastridae		X			
Lysianassidae	X		X		X
Melita dentata	X				X
Melita formosa	X				
Melita quadrispinosa	X				
Melitidae	X				
Metacaprella horrida				X	
Metopa sp.	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Metopa spitzbergensis	X				
Michthyops arctica					X
Monoculodes borealis					X
Monoculodes sp.	X				
Munnopsis sp.			X		
Munnopsis typica	X	X	X		X
Munnopsurus giganteus		X		X	X
Munnopsurus sp.				X	
Mysidae	X		X		X
Nebalia sp.	X				
Neohela monstrosa				X	
Neopleustes pulchellus					X
Nototropis smitti	X	X	X	X	
Oediceros sp.	X				
Onisimus litoralis				X	
Orchomenella sp.	X				
Orchomenopsis obtusus		X			
Pandalus montagui					X
Paralibrotus setosus			X		
Paramphithoe hystrix	X	X	X	X	X
Paramphithoe polyacantha	X				
Paratryphosites abyssi	X		X		
Pardalisca abyssi					X
Pardalisca cuspidata	X			X	X
Pardalisca sp.					X
Parerythrops spectabilis					X
Paroediceros intermedius			X		
Paroediceros lynceus		X	X	X	
Paronesimus barentsi	X	X			
Phippsiella similis		X			X
Pleustes (Pleustes) panoplus					X
Pontoporeia femorata	X	X			
Praunus flexuosus		X			

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Praunus sp.				X	
Protomedeia fasciata	X				
Protomedeia grandimana	X				
Pseudomma affine					X
Pseudomma roseum	X	X			X
Pseudomma sp.		X		X	
Rhachotropis aculeata	X	X	X	X	X
Rhachotropis macropus		X		X	
Rhachotropis oculata	X				
Rhachotropis sp.	X	X		X	
Rozinante fragilis	X		X		
Sabinea septemcarinata	X	X	X	X	X
Sabinea sp.	X	X			
Saduria entomon	X				
Saduria sabini	X	X	X		
Saduria sibirica	X				
Sclerocrangon ferox	X	X		X	X
Socarnes bidenticulatus	X		X		
Spirontocaris intermedia		X			
Spirontocaris phippsii			X		
Spirontocaris spinus	X	X	X	X	X
Stegocephalidae	X				
Stegocephalus inflatus	X	X	X	X	X
Synidotea bicuspida	X	X			
Synidotea marmorata	X	X			
Themisto abyssorum				X	
Themisto libellula	X	X	X	X	X
Themisto sp.			X	X	
Tmetonyx acutus					X
Tmetonyx cicada	X	X	X	X	
Tmetonyx similis		X			
Tmetonyx sp.		X		X	
Tritella pilimana	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Unciola leucopis					X
Unciola sp.					X
Maxillopoda	**X**	**X**	**X**	**X**	**X**
Balanus balanus		X	X		
Balanus crenatus	X	X			
Balanus rostratus		X			
Cirripedia			X		
Scalpellidae	X				
Scalpellum sp.				X	X
Pycnogonida	**X**	**X**	**X**	**X**	**X**
Boreonymphon abyssorum		X	X	X	X
Boreonymphon ossiansarsi					X
Boreonymphon robustum					X
Boreonymphon sp.		X			
Colossendeis angusta			X		
Colossendeis proboscidea			X		X
Eurycyde hispida				X	
Eurycyde sp.				X	
Nymphon brevirostre			X		
Nymphon elegans				X	X
Nymphon grossipes				X	
Nymphon hirtipes	X	X	X	X	X
Nymphon leptocheles		X			
Nymphon longitarse	X	X			
Nymphon macronyx		X			
Nymphon macrum	X	X			
Nymphon serratum				X	
Nymphon sluiteri	X		X		
Nymphon sp.		X			
Nymphon stroemi			X	X	X
Brachiopoda	**X**	**X**	**X**		**X**
Bryozoa	**X**	**X**	**X**	**X**	**X**
Gymnolaemata	**X**	**X**	**X**	**X**	**X**

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Alcyonidium disciforme	X	X	X		
Alcyonidium gelatinosum anderssoni	X	X	X	X	X
Alcyonidium mamillatum		X			
Alcyonidium sp.	X	X			
Alcyonidium sp.C	X		X	X	
Alcyonidium sp.E	X		X	X	
Arctonula arctica				X	
Bowerbankia sp.			X		
Bugula sp.			X		
Bugulidae	X	X			
Callopora craticula					X
Callopora sp.		X	X		
Candidae	X	X	X		
Carbasea carbasea	X		X		
Cauloramphus intermedius	X				
Cellepora smitti				X	
Cellepora sp.	X	X			X
Cheilopora sincera		X		X	X
Cribrilina spitzbergensis	X	X			
Cystisella saccata	X	X		X	X
Cystisella sp.					X
Dendrobeania levinseni	X				
Dendrobeania sp.			X	X	
Doryporella spathulifera		X			
Escharella dijmphnae	X		X		
Escharellidae			X		
Escharoides jacksoni			X		
Escharopsis rosacea		X			
Escharopsis sarsi				X	
Eucratea loricata		X	X	X	X
Eucratea loricata arctica	X				
Flustra sp.			X		
Hippoporina reticulatopunctata	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Kinetoskias arborescens		X			
Kinetoskias sp.	X		X		
Lepralielloidea		X			
Membraniporidae		X	X		
Myriapora sp.	X	X	X	X	
Myriozoella plana	X		X		
Porella sacata			X	X	
Porella smitti	X				
Posterula sarsii				X	X
Pseudoflustra anderssoni					X
Pseudoflustra sinuosa		X	X		
Pseudoflustra solida	X	X	X		X
Pseudoflustra sp.	X	X			
Rhamphostomella costata	X				
Rhamphostomella ovata	X				
Rhamphostomella sp.				X	
Sarsiflustra abyssicola	X	X			
Schizoporella costata				X	
Schizoporella sp.		X		X	
Schizoporellidae	X				
Scrupocellaria sp.		X			X
Semibugula birulai			X		
Smittina jeffreysi			X		
Smittina sp.					X
Tegella armifera	X			X	
Tegella inermis					X
Tegella sp.			X		X
Tricellaria ternata			X		
Stenolaemata	**X**	**X**	**X**		**X**
Crisia sp.			X		X
Cyclostomatida		X			
Idmoneidae	X				
Lichenopora crassiuscula		X			

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Lichenopora sp.		X			
Lichenoporidae	X				
Patinella sp.	X				
Tubulipora sp.					X
Tubuliporidae	X		X		X
Cephalorhyncha	**X**	**X**		**X**	**X**
Priapulida	**X**	**X**		**X**	**X**
Priapulopsis bicaudatus		X		X	
Priapulus caudatus	X			X	X
Priapulus sp.	X				
Cnidaria	**X**	**X**	**X**	**X**	**X**
Anthozoa	**X**	**X**	**X**	**X**	**X**
Acontiaria				X	
Actinauge sp.		X	X	X	X
Actinauge verrillii				X	X
Actiniaria	X	X	X	X	X
Actiniidae		X			
Athenaria		X			X
Bolocera sp.	X				
Ceriantharia			X	X	
Drifa glomerata				X	
Edwardsia sp.	X	X			
Epizoanthidae					X
Hexacorallia					X
Hormathia digitata			X		X
Nephtheidae	X	X	X	X	X
Paraedwardsia arenaria			X		
Scleractinia				X	
Stephanauge sp.					X
Subsessiliflorae				X	
Zoanthidae		X		X	X
Hydrozoa	**X**	**X**	**X**	**X**	**X**
Bonneviellidae				X	

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Bougainvillia sp.			X		
Campanulariidae	X	X			
Campanulinidae				X	X
Eudendriidae		X	X		
Eudendrium sp.	X		X		
Filellum serpens		X		X	X
Halecium beanii				X	
Halecium sp.					X
Hydractinia allmani			X		
Lafoea dumosa		X	X		X
Lafoea sp.			X		X
Lafoeidae	X		X	X	X
Lafoeina maxima	X	X		X	X
Lafoeina sp.			X		
Obelia longissima		X			
Obelia loveni	X				
Obelia sp.	X				X
Sertularia sp.		X		X	
Sertulariidae	X		X		
Stegopoma plicatile			X		
Stegopoma sp.	X	X		X	X
Symplectoscyphus tricuspidatus					X
Thuiaria sp.			X		X
Echinodermata	**X**	**X**	**X**	**X**	**X**
Asteroidea	**X**	**X**	**X**	**X**	**X**
Asterias sp.	X				
Bathybiaster vexillifer					X
Crossaster papposus	X	X	X	X	X
Ctenodiscus crispatus	X	X	X	X	X
Henricia sp.			X	X	X
Hymenaster pellucidus		X		X	X
Hymenaster sp.		X			
Icasterias panopla	X	X		X	X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Korethrasteridae				X	
Leptasterias groenlandica		X			
Leptasterias sp.	X	X			
Lethasterias sp.			X		
Lophaster furcifer				X	X
Lophaster sp.		X			
Pontaster tenuispinus	X	X	X	X	X
Porania (Porania) pulvillus		X			
Poraniomorpha sp.		X	X		
Poraniomorpha tumida			X		
Psilaster andromeda				X	X
Pteraster militaris				X	
Pteraster obscurus	X				
Pteraster pulvillus				X	X
Spinulosida				X	
Urasterias lincki		X	X	X	
Valvatacea					X
Crinoidea	**X**	**X**	**X**	**X**	**X**
Antedonidae		X			X
Bourgueticrinina	X				X
Hathrometra tenella				X	X
Heliometra glacialis		X	X	X	X
Poliometra prolixa	X	X	X	X	X
Echinoidea	**X**	**X**	**X**	**X**	**X**
Pourtalesia sp.	X		X		
Strongylocentrotus sp.		X		X	X
Holothuroidea	**X**	**X**	**X**	**X**	**X**
Cucumaria frondosa			X		
Cucumaria sp.		X			
Cucumariidae	X	X	X		X
Dendrochirotida	X	X	X	X	X
Elpidia belyaevi			X	X	X
Elpidia sp.					X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Eupyrgus scaber			X		
Molpadida			X		
Molpadiidae				X	
Myriotrochus rinkii	X				
Myriotrochus sp.		X	X	X	X
Psolus fabricii		X			
Psolus sp.		X	X		
Ophiuroidea	**X**	**X**	**X**	**X**	**X**
Amphiura sp.	X	X			X
Amphiura sundevalli		X			
Amphiuridae				X	
Gorgonocephalus arcticus		X	X	X	
Gorgonocephalus arcticus/eucnemis					X
Gorgonocephalus eucnemis	X			X	X
Gorgonocephalus sp.					X
Ophiacantha bidentata	X	X	X	X	X
Ophiacantha sp.	X				
Ophiactidae	X				
Ophiocten sericeum	X	X	X	X	X
Ophiocten sp.	X				
Ophiopholis aculeata				X	X
Ophiopleura borealis	X	X	X	X	X
Ophiopus arcticus			X	X	X
Ophioscolex glacialis			X	X	X
Ophiura robusta	X	X	X	X	X
Ophiura sarsii		X		X	X
Ophiura sp.	X				X
Stegophiura nodosa		X			
Entoprocta		**X**			
Mollusca	**X**	**X**	**X**	**X**	**X**
Bivalvia	**X**	**X**	**X**	**X**	**X**
Acanthocardia echinata		X			
Astarte borealis	X	X			X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Astarte crenata		X	X	X	X
Astarte montagui	X	X	X	X	X
Astarte sp.	X	X		X	
Axinopsida sp.		X			
Bathyarca glacialis	X	X	X	X	X
Bathyarca sp. (< 1.5 cm)	X	X	X	X	X
Chlamys islandica		X			
Ciliatocardium ciliatum ciliatum	X	X		X	
Ciliatocardium sp.		X			
Cuspidaria glacialis	X	X		X	X
Cuspidaria rostrata		X			
Cuspidaria sp.	X			X	
Cyclopecten hoskynsi			X		X
Cyrtodaria siliqua	X				
Ennucula tenuis	X	X	X	X	X
Hiatella arctica	X	X	X	X	
Limatula subauriculata		X			
Liocyma fluctuosa	X				
Lyonsia arenosa	X	X	X		
Lyonsiella sp.	X			X	
Macoma brota	X				
Macoma calcarea	X	X	X		
Macoma moesta	X				
Macoma torelli					X
Megayoldia thraciaeformis					X
Montacuta sp.	X				
Musculus discors	X	X	X	X	X
Musculus niger	X		X	X	X
Musculus sp.		X			
Mya sp.	X				
Nucula pusilla		X			
Nuculana minuta			X	X	
Nuculana pernula	X	X	X	X	X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Nuculana sp.	X				
Pandora glacialis	X		X		
Panomya norvegica		X			
Periploma sp.	X			X	
Portlandia arctica		X	X		
Portlandia intermedia		X	X	X	X
Portlandia sp.	X	X		X	X
Serripes groenlandicus	X				
Similipecten greenlandicus	X	X	X	X	X
Thraciidae			X		
Thyasira gouldi				X	X
Thyasira sp.	X		X	X	X
Yoldia hyperborea	X	X	X		
Yoldia sp.	X	X		X	
Yoldiella frigida			X		
Yoldiella lenticula	X		X		
Yoldiella sp.		X			X
Caudofoveata		**X**	**X**	**X**	**X**
Chaetodermatida		X	X	X	X
Cephalopoda	**X**		**X**	**X**	**X**
Bathypolypus arcticus				X	X
Rossia palpebrosa			X		
Rossia sp.					X
Semirossia tenera	X				
Gastropoda	**X**	**X**	**X**	**X**	**X**
Acmaea sp.	X				
Acmaeidae					X
Admete sp.	X				
Admete viridula		X			X
Ariadnaria borealis	X		X		X
Aulacofusus brevicauda					X
Beringius ossianius		X			
Boreotrophon clathratus	X				

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Boreotrophon pacificus	X				
Boreotrophon sp.	X	X			X
Boreotrophon truncatus		X			
Buccinidae				X	
Buccinum angulosum	X	X			
Buccinum belcheri			X		X
Buccinum ciliatum	X	X			
Buccinum ciliatum sericatum	X	X			
Buccinum cyaneum	X				
Buccinum glaciale/angulosum	X				
Buccinum hydrophanum		X	X	X	X
Buccinum micropoma			X		
Buccinum plectrum	X				
Buccinum polare	X	X			
Buccinum scalariforme	X	X			
Buccinum sp.		X	X		
Clione limacina			X		
Colus holboelli			X	X	X
Colus islandicus			X		
Colus latericeus	X				
Colus pubescens	X	X	X	X	X
Colus sabini	X	X	X		X
Cryptonatica affinis	X	X	X		X
Curtitoma decussata	X				X
Curtitoma incisula	X	X			
Cylichna alba	X		X	X	X
Cylichna occulta	X		X		
Cylichna sp.	X	X			
Diaphana globosa	X				
Lepeta caeca		X	X	X	X
Lepeta sp.					X
Limneria undata			X	X	
Lunatia pallida	X	X	X	X	X

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Lunatia sp.	X				
Mangeliidae					X
Margarites costalis	X	X	X		X
Margarites groenlandicus	X	X			
Margarites groenlandicus umbilicalis	X		X		
Margarites olivaceus			X		
Margarites sordidus	X				
Margarites sp.	X				
Mitrella sp.					X
Neptunea despecta		X	X		X
Neptunea heros		X			
Neptunea intersculpta					X
Neptunea ithia	X				
Neptunea sp.	X			X	
Nodulotrophon coronatus	X				
Nudibranchia	X				
Nudibranchia A	X				
Nudibranchia C	X				
Odostomia sp.		X			
Odostomiinae	X				
Oenopota bicarinata	X				
Oenopota cinerea	X				
Oenopota obliqua					X
Oenopota sp.			X		X
Philine quadrata			X	X	
Philine sp.		X	X		
Piliscus commodus			X		
Plicifusus kroeyeri	X				
Praephiline finmarchica			X	X	
Propebela turricula/nobilis	X				
Scabrotrophon fabricii				X	X
Solariella sp.	X				
Tachyrhynchus erosus	X	X			

Phylum **Class** **Taxon**	**Beaufort Sea**	**Amundsen Gulf**	**Western Archipelago**	**Eastern Archipelago**	**Baffin Bay**
Testudinalia testudinalis		X			
Trichotropis bicarinata			X		X
Turridae			X	X	
Turrisipho lachesis			X		X
Velutina sp.	X			X	
Volutomitra groenlandica					X
Volutopsius norwegicus				X	
Scaphopoda	**X**	**X**	**X**	**X**	
Siphonodentalium lobatum	X	X	X	X	
Nemertea	**X**	**X**	**X**	**X**	**X**
Platyhelminthes	**X**	**X**		**X**	**X**
Porifera	**X**	**X**	**X**	**X**	**X**
Sipuncula	**X**	**X**	**X**	**X**	**X**
Sipunculidea	**X**	**X**	**X**	**X**	**X**
Golfingia sp.		X	X	X	X
Golfingiidae	X	X			
Phascolion sp.	X	X	X	X	X
Phascolionidae	X		X		
Sipunculidae	X	X	X		X

CHAPITRE 2

FACTEURS ENVIRONNEMENTAUX STRUCTURANT LES COMMUNAUTÉS DE LA MÉGAFAUNE BENTHIQUE DE L'ARCTIQUE CANADIEN

RÉSUMÉ

Les gradients environnementaux et leur pouvoir explicatif sur la structure des communautés benthiques varient à différentes échelles spatiales. Toutefois, peu d'études dans l'Arctique ont tenté d'étudier l'influence de gradients environnementaux variant à diverses échelles spatiales sur une aire d'étude à l'échelle continentale. Le projet actuel a étudié pour la première fois comment la structure des communautés mégabenthiques répond à plusieurs facteurs environnementaux sur une région de 2 000 km dans l'Arctique canadien, de la mer de Beaufort jusqu'au nord de la baie de Baffin. Les communautés ont été échantillonnées avec un chalut scientifique Agassiz entre 2007 et 2011 à 78 stations situées entre 30 et 1 000 m de profondeur. La force des relations statistiques entre diverses caractéristiques des communautés (ex. biomasse, densité, richesse, diversité et composition taxonomique) et divers gradients environnementaux (ex. directs, indirects/spatiaux et des ressources) a été examinée. Six communautés mégabenthiques ont été définies en fonction de leur composition taxonomique. Leur distribution était significativement, mais modérément, associée d'une part à des gradients environnementaux variant à grande échelle (100-1000 km; ex. profondeur, variables océanographiques) et d'autre part associée à des gradients environnementaux variant à une méso échelle (10-100 km ; ex. type de substrat, carbone organique dans les sédiments). Nous n'avons pas observé une forte baisse de la biomasse, densité et richesse en fonction de la profondeur, ni une forte augmentation des caractéristiques des communautés avec les indicateurs des ressources alimentaires, contrairement à notre hypothèse. Nous discutons comment des conditions

environnementales locales à régionales, telles que des régimes de courants ou la présence de polynies, maintiennent de fortes biomasses benthiques dans des régions oligotrophes et profondes de l'Arctique canadien. Cette étude démontre l'importance de considérer les échelles de variabilité des gradients environnementaux lors de l'interprétation de leurs effets sur la structure des communautés.

Ce deuxième article, intitulé « *Environmental drivers of the Canadian Arctic megabenthic communities* » fut corédigé par moi-même, les professeurs Katrin Iken et Philippe Archambault. Il fut accepté pour publication dans sa version finale en mai 2014 par les éditeurs du journal *PLoS ONE* et fut publié en ligne en juillet 2014. En tant que première auteur, ma contribution à ce travail fut l'essentiel de la recherche bibliographique, l'échantillonnage, les analyses de laboratoire, le traitement statistique des résultats et la rédaction de l'article. Le professeur K. Iken a contribué à l'approche statistique et a aidé à la révision de l'article. Le professeur P. Archambault a contribué à l'idée originale, à l'approche statistique et a aidé à la révision de l'article. Une version abrégée de cet article a été présentée à la *World Conference on Marine Biodiversity* à Aberdeen (Écosse) à l'automne 2011, ainsi qu'à trois reprises à l'automne 2012 lors de la *Réunion annuelle de CHONe* à Ottawa (Canada), de *l'Assemblée générale annuelle de Québec-Océan* à Montréal (Canada) et à la *Réunion scientifique annuelle ArcticNet* à Vancouver (Canada).

ENVIRONMENTAL DRIVERS OF THE CANADIAN ARCTIC MEGABENTHIC COMMUNITIES

ABSTRACT

Environmental gradients and their influence on benthic community structure vary over different spatial scales; yet, few studies in the Arctic have attempted to study the influence of environmental gradients at differing spatial scales on megabenthic communities across continental-scales. The current project studied for the first time how megabenthic community structure is related to several environmental factors over 2000 km of the Canadian Arctic, from the Beaufort Sea to northern Baffin Bay. Faunal trawl samples were collected between 2007 and 2011 at 78 stations from 30 to 1000 m depth and patterns in biomass, density, richness, diversity and taxonomic composition were examined in relation to indirect/spatial gradients (e.g., depth), direct gradients (e.g., bottom oceanographic variables), and resource gradients (e.g., food supply proxies). Six benthic community types were defined based on their biomass-based taxonomic composition. Their distribution was significantly, but moderately, associated with large-scale (100-1000 km) environmental gradients defined by depth, physical water properties (e.g., bottom salinity), and meso-scale (10-100 km) environmental gradients defined by substrate type (hard *vs.* soft) and sediment organic carbon content. We did not observe a strong decline of bulk biomass, density and richness with depth or a strong increase of those community characteristics with food supply proxies, contrary to our hypothesis. We discuss how local- to meso-scale environmental conditions, such as bottom current regimes and polynyas, sustain biomass-rich communities at specific locations in oligotrophic and in deep regions of the Canadian Arctic. This study demonstrates the value of considering the scales of variability of environmental gradients when interpreting their relevance in structuring of communities.

***Keywords*:** Arctic, benthos, megafauna, environmental drivers, community structure, spatial scale, depth, oceanographic variables, water mass, food supply, polynya, sediment pigments, sediment organic carbon, current regimes.

INTRODUCTION

In Arctic systems, megabenthic communities contribute significantly to bulk benthic biomass (Piepenburg & Schmid 1996; Bluhm *et al.* 2009) with high oxygen demands (Piepenburg & Schmid 1996, 1997; Ambrose *et al.* 2001; Renaud *et al.* 2007a) and important roles in carbon cycling on Arctic shelves (Grebmeier *et al.* 1995; Klages *et al.* 2004). Megabenthic communities also provide an important link to higher trophic levels as food for many sea birds and marine mammals (Stirling 1997; Bluhm & Gradinger 2008). Despite their importance in Arctic food webs, little is still known, however, about their distributional patterns and the environmental factors driving them across the large spatial extents, such as the Canadian Arctic Archipelago.

The external drivers of benthic community dynamics change with the spatial scale under investigation. At small scales (e.g., within a sampling station), community structure is controlled mainly by ecological factors such as the availability of niches superimposed by competition and predation, while at meso (10-100 km) to large (100-1000 km) scales it is mainly controlled by environmental gradients (Zajac *et al.* 1998; Levin *et al.* 2001; Piepenburg 2005; Gray & Elliott 2009). Depth and geographic gradients generate large-scale benthic patterns that are well known in the World's oceans (Snelgrove 2001; McArthur *et al.* 2010). For Arctic megafaunal communities, depth is often considered one of the most important large-scale structuring variables (Piepenburg *et al.* 1996; Piepenburg & Schmid 1996; Jones *et al.* 2007; Soltwedel *et al.* 2009; Wei *et al.* 2010; Bluhm *et al.* 2011a). However, depth is mostly a proxy of other environmental variables that vary vertically, such as physical properties of water masses (temperature, salinity) and declining food availability for slope and deep-sea benthic communities (Smith *et al.* 2008). In the highly seasonal Arctic systems, the declining strength of pelagic-benthic coupling and the resultant reduced food supply is thought to be the most important indirect effect of depth in structuring benthic communities (Klages *et al.* 2004; Soltwedel *et al.* 2009) and benthic processes (Forest *et al.* 2011). In contrast to large-scale gradients, patterns in current regimes and sea-ice cover, by their influence on primary production and on the sedimentation of organic matter out of the water column, produce meso-scale benthic patterns that are typically regionally specific, such as under polynyas and marginal ice zones in the Arctic (Piepenburg 2005). In the quest to elucidate the importance of food supply on Arctic benthic communities, and because of the complexity of biological and physical interactions that can increase or reduce pelagic-benthic coupling, various food supply proxies are often used to interpret benthic community patterns (Carroll & Ambrose 2012). This study tested a variety of food supply proxies, from estimates of particulate organic carbon (POC) fluxes (e.g., derived from primary productivity in surface waters) to estimates of available organic matter for benthic organisms (e.g., sediment pigment). Substrate variability is also an important local- to meso-scale driver of megabenthic taxonomic composition in both Arctic shelf and slope regions (Mayer & Piepenburg 1996; Bluhm *et al.* 2009). By reflecting near-bottom flow regime, substrate variability influences benthic feeding modes and survival of organisms due to specific requirements from larvae to adult stages (Snelgrove & Butman 1994), and thus profoundly affects benthic community composition.

The Canadian Arctic is an excellent candidate area to test whether large-scale and meso-scale environment-benthic community relationships found elsewhere across the world's oceans also apply within a large, topographically and hydrographically complex Arctic marine environment. The Canadian Arctic is characterized by great depth variation, complex flow dynamics (McLaughlin *et al.* 2004), contrasting biological productivity regimes (Ardyna *et al.* 2011), and significant freshwater and sediment inflow from the Mackenzie River, by far the most sediment-rich river discharging into the Arctic Ocean (O'Brien *et al.* 2006).

The current project studied how megabenthic community structure is associated with environmental gradients across 70° longitude (2000 km) of the Canadian Arctic marine environment. The specific objectives of this study were: (1) to delineate community clusters and characterize their structure and distribution patterns, and (2) to evaluate the relationships of environmental factors of various spatial scales to megabenthic community characteristics (e.g., richness, biomass) and community distribution. We hypothesized that: (i) megabenthic biomass, density, richness and diversity decrease with depth and increase with food supply proxies, and (ii) community patterns are associated primarily with large-scale environmental gradients (100-1000 km), and secondarily with meso-scale gradients (10-100 km). This study increases our understanding of the Arctic that is experiencing rapid changes and could serve as a benchmark against which future changes in megabenthic diversity and community patterns could be identified (e.g., species range shifts, invasive species).

MATERIALS AND METHODS

Study area

This study was conducted across the Canadian Arctic from the Mackenzie Shelf in the southeastern Beaufort Sea in the west (135°W) to northern Baffin Bay in the east (65°W) (Figure 13). The two main water masses flowing through the Canadian Arctic originate mainly from the Pacific and Atlantic oceans. The colder-fresher Pacific-origin waters (on average < 200 m depth) overlie the warmer-saline Atlantic-origin waters below (on average > 200 m depth) (McLaughlin *et al.* 2004). The transition between these water masses coincides generally across the study area with the 200 m isobath along the shelf break (O'Brien *et al.* 2006; Spalding *et al.* 2007). The Beaufort Sea and Amundsen Gulf regions are highly influenced by the Mackenzie River that drains a watershed of 1.7×10^6 km^2 and discharges approximately 340 km^3 y^{-1} of freshwater (McLaughlin *et al.* 2004) and 127×10^6 Mt y^{-1} of sediment load (Macdonald *et al.* 2004) into the Beaufort Sea. The complex topography of the Canadian Arctic Archipelago with its numerous islands and channels has a profound influence on sea ice circulation and marine biological productivity regimes (Michel *et al.* 2006). During winter the study area is ice-covered and sea ice could be found throughout the summer as landfast ice or first-year and multiyear pack ice (Howell *et al.* 2009; EC 2010). Summer sea ice distribution along with ice break-up and freeze-up dates exhibit large inter-annual variations (Howell *et al.* 2009; EC 2010). As a general trend, ice in summer remains longer in the central part of the Archipelago than in areas where large and latent heat polynyas open in spring, such as the North Water (NOW), Lancaster Sound-Bylot Island (LS-BI), and the Cape Bathurst (CB) polynyas (Michel *et al.* 2006; Howell *et al.* 2008) (Figure 13). Polynyas located in the northeastern Canadian Arctic (i.e., NOW and LS-BI) exhibit intense marine biological productivity and tight pelagic-benthic coupling as revealed by field observations of diatom-based communities (Ardyna *et al.* 2011), satellite-derived high annual primary production (PP) estimates (Bélanger *et al.* 2013), and high sediment chlorophyll *a* (Chl *a*) concentrations and benthic boundary fluxes (Kenchington *et al.* 2011; Link *et al.* 2013b). In the CB polynya, in contrast, highly variable intensity, timing and duration of phytoplankton blooms (Arrigo & van Dijken 2004), and strong grazing pressure by zooplankton leads to weak pelagic-benthic coupling (Conlan *et al.* 2008; Darnis *et al.* 2012; Link *et al.* 2013b). The central Archipelago has been defined as an oligotrophic system (Ardyna *et al.* 2011).

Ethics Statement

Sampling licenses were obtained for the Northwest Territories (Canada) by the Aurora Research Institute (#14258, #14304, #14543, #14678, #14917), by the Environmental Impact Screening Committee (#06 07 05, #06 03 10, #03 09 03), and by the Department of Fisheries and Oceans (DFO) (#S-07/08-4017-IN, #S-09/10-4013-IN, #S-10/11-3026-YK, #S-11/12-3026-YK). For Nunavut (Canada) permits were provided by the Nunavut Research Institute (#0500907R-M, #0501408R-M, #0504609R-M, #0505510R-M, #0506511R-M) and by DFO (S-07/08-1034-NU, #S-08/09-1043-NU, # S-09/10-1049-NU, #S-10/11-1021-NU, #S-11/12-1029-NU).

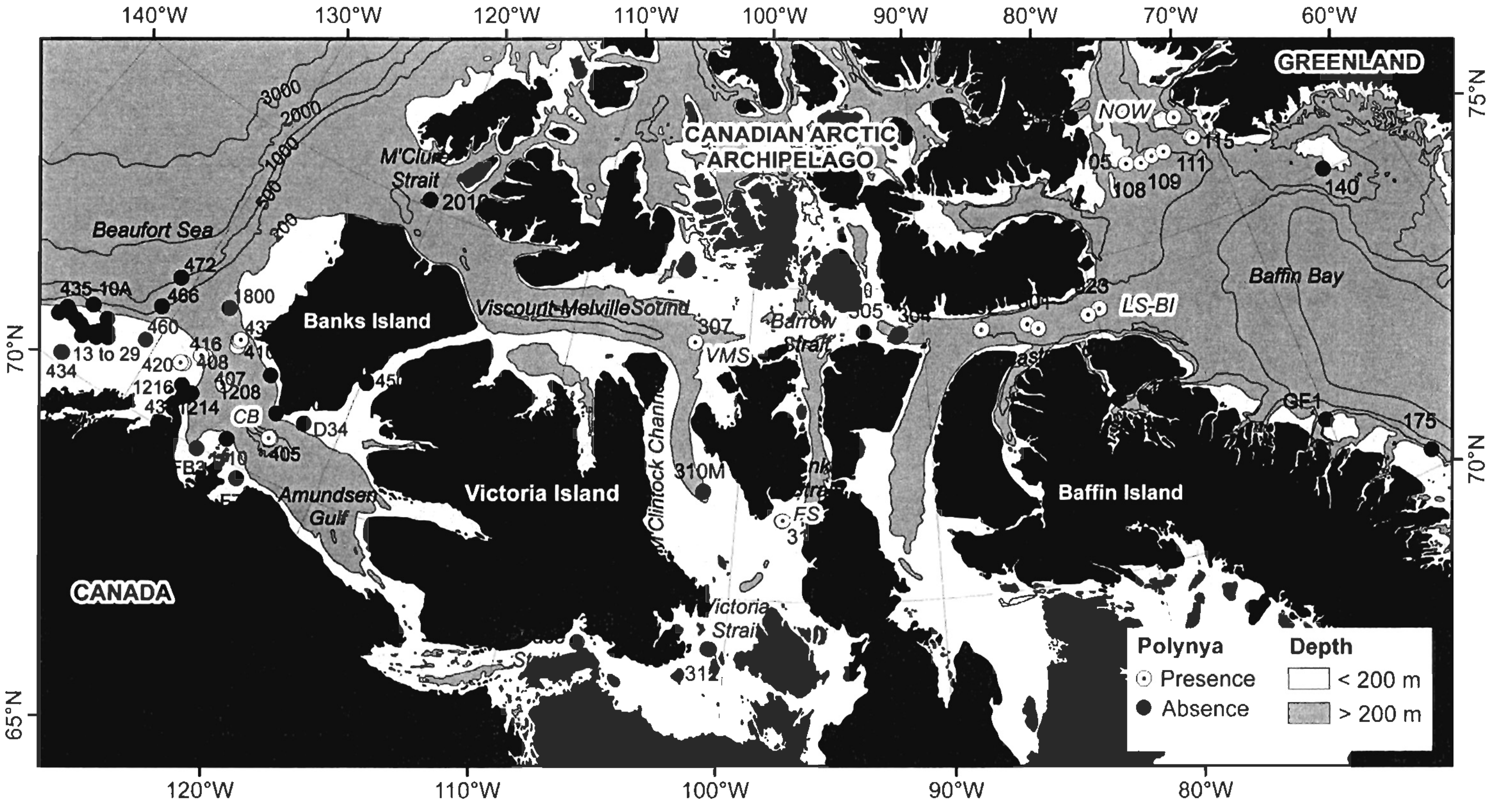

Figure 13. Locations of stations sampled from 2007 to 2011 across the Canadian Arctic. Stations sampled in areas where polynyas are recurrently present (white circles) or absent (black circles). Station codes correspond to ArcticNet expedition labels, sampling years were not added for clarity. Names of polynyas are indicated by capital italic letters (*CB*: Cape Bathurst polynya, *FS*: Franklin Strait polynya, *LS-BI*: Lancaster Sound-Bylot Island polynya, *NOW*: North Water polynya, *VMS*: Viscount-Melville Sound polynya). The shelf break and the transition between the Pacific and Atlantic water masses are both around 200 m (< 200 m: shelf and Pacific layer; > 200 m: slope and Atlantic layer).

Faunal data collection

Benthic megafauna were sampled at 78 stations between June and October from 2007 to 2011 onboard the Canadian research icebreaker CCGS *Amundsen* (Figure 13). Station depths ranged from 34 to 1024 m, all below the average ice scouring zone (Gutt 2001; O'Brien *et al.* 2006). All faunal samples were collected with an Agassiz trawl (effective opening of 1.5 m and a 40 mm net mesh size, with a 5 mm cod end liner) with average trawling time and speed of 5 min and 1.5 knots, respectively. In order to standardize community characteristics among stations (by m^2), bottom trawling time and vessel speed at each station were used to calculate towed area (trawl opening of 1.5 m × distance towed; average trawled area of 372 ± 161 m^2). This trawl design is very effective at collecting both epibenthic and burrowing, large-sized invertebrates. Based on the methodology of Piepenburg *et al.* (1996), invertebrates larger than 2 cm were sorted from the trawl catches directly after capture and classified as megabenthos. In addition, the sediment contained in the catches was washed through a 2 mm sieve under running seawater onboard (Piepenburg *et al.* 1996). Planktonic invertebrates that were accidentally taken by the trawl (e.g., Chaetognatha, Euphausiacea, Scyphozoa) and Pisces were removed to only include benthic invertebrates in the sample analysis. Members of the class Ascidiacea were not considered in this study due to exclusion of this taxon during the first years of sampling. Only large echinoderm taxa that could be reliably identified to species level were counted and wet-weighed in the field given the low precision of on-board mass measurements (detection limit of 5 g). All other taxa were preserved in a 4 % seawater-formaldehyde solution buffered with sodium tetraethylborate or frozen for later identification in the lab, and their biomass was determined as formaldehyde wet mass or wet mass (after thawing) at 0.001 g precision. Possible biases in total biomass calculations introduced by different preservation methods were considered minor since all specimens within a phylum were processed the same way and trawl catches were considered semi-quantitative estimates (Eleftheriou & McIntyre 2005; Wetzel *et al.* 2005). Only specimens with the head-part intact were counted and identified to the lowest possible taxonomic level. However, some taxa were left at the phylum level because no complete identification keys exist for Canadian Arctic waters (e.g., Brachiopoda, Nemertea, Platyhelminthes, Porifera); we acknowledge that their richness will have been underestimated in this study. Taxonomic names were verified using the World Register of Marine Species (WoRMS, Appeltans *et al.* 2013). Four species of the phylum Bryozoa and one from the phylum Hydrozoa were not listed in WoRMS but were verified using the Integrated Taxonomic Information System (ITIS, www.itis.gov) (i.e., Bryozoa: *Cellepora smitti, Escharopsis rosacea, Escharopsis sarsi, Porella sacata;* Hydrozoa: *Obelia loveni*).

Environmental data collection

Explanatory environmental variables available for the present study were divided into three categories: resource, direct and indirect/spatial gradients (following McArthur *et al.* 2010). Resource gradients included estimates of vertical POC fluxes derived from primary productivity in surface waters (e.g., phytoplankton biomass, PP estimates) to sediment variables that were proxies of the energy available for benthic consumers (e.g., sediment pigments, sediment organic carbon). Resource gradient variables are called hereafter 'food supply proxies'. Direct gradients included bottom oceanographic variables (i.e., temperature, oxygen, salinity), seabed substrate type (hard *vs.* soft) and terrestrial influence on the benthic habitat (i.e., sediment $\delta^{13}C$), these variables selecting for the type of physiology, morphology and/or life history of species residing there. Finally, indirect/spatial gradients consisted of purely spatial variables (depth, latitude and longitude) that often correlate with direct and resource variables but with no direct physiological influence on the species. All these environmental gradient categories vary on different temporal scales and we assessed their temporal variability as follow. Spatial variables were assumed temporally stable, except on geological time scales. Direct variables were overall assumed to be unchanging on less than a decadal scale (Michel *et al.* 2006). Food supply proxies fluctuate either on a seasonal basis (e.g., phytoplankton biomass (Ardyna *et al.* 2011) and sediment Chl *a* (Morata *et al.* 2008; Link *et al.* 2011)) or on a multi-annual basis (e.g., PP estimates integrated over years, sediment organic carbon (Magen *et al.* 2010; Bailey *et al.* 2013)). Additionally, these environmental categories exhibit measurable heterogeneity at different spatial scales, from study area extent to distance between stations. In a continental-scale study such as this one, indirect/spatial and direct gradients should mostly influence benthic community patterns over large geographic scales (100-1000 km), while resource gradients should induce environmental heterogeneity mainly at meso-geographic scales (10-100 km) (Piepenburg 2005).

Food supply proxies - primary productivity

We used pelagic primary productivity estimates as food supply proxies for benthic organisms based on the assumption that areas with higher pelagic primary productivity should generally have higher vertical POC fluxes (McArthur *et al.* 2010). We consequently evaluated if the spatial variability in primary productivity of surface waters was linked to the spatial variability observed in benthic community patterns. Various estimates of primary productivity differ in their temporal integration of the variability of a system. For seasonal variability, we used phytoplankton biomass estimates based on water Chl *a* concentrations measured at the time and locations of faunal sampling and integrated over the euphotic zone (from surface to 0.2 % surface light level). We also tested if different size fractions of phytoplankton biomass estimates would be linked with the same strength to benthic community patterns, as large cells sink rapidly and are therefore supposed to contribute most to the carbon flux reaching the seafloor (Wassmann 1998). We estimated the following phytoplankton biomass size fractions: euphotic B_T = total phytoplankton biomass (cells ≥ 0.7 µm; mg Chl *a* m^{-2}); euphotic B_S = biomass of small phytoplankton cells (0.7–5 µm; mg Chl *a* m^{-2}); euphotic B_L = biomass of large phytoplankton cells (≥ 5 µm; mg Chl *a* m^{-2}); and euphotic B_L:B_T = relative contribution of large cells to total biomass. Data were available at 73 stations and details on the sampling and analytical methods are found in Ardyna *et al.* (2011). In addition, we summed satellite-derived monthly PP estimates to assess annual variability of primary productivity. Sums of monthly PP estimates over one (PP 1Y) and five years (PP 5Y) before faunal sampling were determined for a 20 km radius around each sampling station based on model results of Bélanger *et al.* (2013) (data available for 71 stations). Sampling stations were also categorized according to presence (n = 30 stations) and absence (n = 48 stations) of a polynya (based on Arrigo and van Dijken 2004 and Barber and Massom 2007) as a proxy of ice conditions and primary productivity.

Food supply proxies - surface sediment

We evaluated the seasonal contribution of 'fresh' organic matter inputs to the benthos as sediment Chl *a* and phaeopigments (degraded chlorophyll) concentrations, and by using sediment organic carbon as an estimate of average annual input. From 2008 to 2011, a USNEL box corer (0.25 m^2) was deployed for collecting surface sediments (upper 1 cm) in triplicate using a 60 ml disposable syringe (2.6 cm diameter with a cut off anterior end). Sediment samples for pigment concentration (Chl *a* and phaeopigments) and organic carbon content were immediately frozen at -80 °C and -20 °C, respectively, for later analysis in the lab. Pigment concentrations were analysed fluorometrically following a modified protocol by Riaux-Gobin and Klein (1993) and are expressed as microgram pigment per gram of dry sediment. Sediment organic carbon content was determined after acidification (HCl 10 %) with a Costech 4010 elemental analyser (Marine Chemistry and Mass Spectrometry Laboratory, Université du Québec à Rimouski, Canada). Sediment organic carbon content is expressed as % of total sediment dry weight.

Terrestrial organic matter input

Sediment $\delta^{13}C$ was used as a measure of the contribution of terrestrial organic carbon input in order to investigate influence of coastal erosion and river sediment discharge on the benthic community structure. Sediment samples were collected and preserved the same way as sediment organic carbon described above. Sediment $\delta^{13}C$ was determined after acidification (HCl 10 %) with a CF-IRMS (continuous-flow Isotope Ratio Mass Spectrometry) (Marine Chemistry and Mass Spectrometry Laboratory, Université du Québec à Rimouski, Rimouski, Québec, Canada) and is reported in standard delta notation in ‰ with respect to VPDB (Vienna Pee Dee Belemnite). Lighter sediment isotopic $\delta^{13}C$

values (-28 to -26 ‰) are typical of terrigenous organic matter while heavier isotopic $\delta^{13}C$ values (-24 to -20 ‰) are typical of marine production (Stein & Macdonald 2004).

Bottom oceanographic variables

Bottom water characteristics were measured at all stations from 2007 to 2011. Near-bottom water temperature (°C), salinity and dissolved oxygen concentration (ml l^{-1}) were determined by the shipboard CTD Seabird™ profiler (SBE911 Plus), combined with a SBE 43 dissolved oxygen sensor, at 10 m above the seafloor.

Substrate type

Because sediment particle size samples could not be consistently sampled during all years, we instead used a qualitative classification based on visual observations of trawls and box corers to assess the substrate type at each station. Substrate category 'hard' was assigned to stations with substantial amounts of gravel and cobbles, and 'soft' assigned to stations with mud (silt and clay), sand and no or little gravel. Overall, fewer hard substrate stations (19 of 78 total stations) were sampled to avoid damaging the trawl and box corer, so that hard bottom stations are under-represented in this study. Near-bottom current speed could not be assessed for this study, but substrate type may be regarded as a proxy for current velocity with coarser substrate indicating a higher near-bottom flow regime (Snelgrove & Butman 1994).

Data analysis

Benthic community characteristics considered in this study for each of the 78 stations were biomass (g m^{-2}), density (ind. m^{-2}), and four biodiversity metrics (taxonomic richness density ($S_{density}$, number of taxa 1000 m^{-2}), Shannon-Wiener's diversity index (H', using $\log_e$), Pielou's evenness index (J'), and average taxonomic distinctness (Δ^*)). H', J' and Δ^* were calculated based on biomass data including colonial taxa. Density was calculated after removal of colonial taxa because their abundance cannot be recorded (i.e., Bryozoa, Hydrozoa, Nephtheidae (soft corals), Porifera). Δ^* estimates the average distance between two randomly chosen organisms through Linnean taxonomy and is considered to be a more genuine reflection of biodiversity than the other diversity indices because it considers taxonomic relationships (Clarke & Warwick 2001). Six taxonomic levels were used in Δ^* calculations: species, genus, family, order, class and phylum, assuming equal step weights between successive taxonomic levels; when necessary, the lowest taxonomic level available was used for missing level(s) (performed using PRIMER-E software version 6; Clarke & Gorley 2006). Correlations between benthic community characteristics and quantitative environmental variables were assessed using Spearman rank correlations to investigate the intensity of all possible relations following a positive or negative monotonic trend (Quinn & Keough 2002). Prior to correlation analysis, we verified by visual observation that no relationship was quadratic (hump-shape curve). Simple linear regressions were performed to model the relationships between benthic community characteristics and depth as an environmental proxy measure often used in benthic studies. Normality of residuals was examined by plotting theoretical quantiles *vs.* standardized residuals (Q-Q plots) and homogeneity of variance was assessed by plotting residual *vs.* fitted (predicted) values. Mann-Whitney *U* tests were used to seek differences in benthic community characteristics between the environmental categories substrate type (hard *vs.* soft) and polynya (presence *vs.* absence). Kruskal-Wallis tests with post-hoc multiple comparison tests were carried out to test differences among community clusters (see below).

For multivariate analyses, lists of taxa at each station were scaled at the genus level and taxa only found at one station were discarded, for a total of 303 unique taxa found at least at two stations. Singletons in multivariate analysis are prone to random and uninterpretable fluctuations, and it is consequently suggested to remove them to allow better detection of the underlying community similarities (Clarke & Warwick 2001). Scaling at the genus level was done because identifications were patchy at the species level among stations; in some cases, specimens were incomplete and missing criteria prevented identification at the species level. Bray-Curtis dissimilarity was calculated for the fourth-root-transformed biomass matrix rather than for the density matrix to be able to include colonial taxa. The fourth-root transformation was chosen to balance the effects of high- and low-biomass taxa to assess responses of the whole communities (Clarke & Warwick 2001). The dissimilarity matrix was then subjected to a hierarchical cluster analysis using Ward's minimum variance method, which seeks to define well-delimited groups by minimizing within-cluster sum of squares (Ward 1963). Community clusters were determined by selecting a distance where stations were fused in well-defined clusters. To find indicator taxa within each community cluster, the indicator value index (IndVal) method of Dufrêne and Legendre (1997) was applied on the biomass data matrix. IndVal is a measure of association between a taxon and a cluster of stations and is calculated as the product of specificity (mean biomass of a given taxon within a cluster compared to the other clusters) and fidelity (taxon occurrence at stations belonging to a cluster). IndVal is maximal (= 100 %) when a given taxon is observed at all stations of only one community cluster and in none of the other clusters. Statistical significances of indicator taxa were tested by random permutation of stations (9999 permutations) and only the five significant indicator taxa with the greatest IndVal value are discussed per community cluster. The influence of all environmental variables on the taxonomic composition was tested on 50 stations (out of 78 stations total) by the use of redundancy analysis (RDA), a direct extension of regression analysis to model multivariate response data. The other 28 stations had to be removed (2007: all 10 stations; 2008: n = 9; 2009: n = 1; 2010 n = 3: 2011: n = 5) because of some missing food supply proxies. A Principal Component Analysis (PCA) plot showing the multivariate similarity among the 50 stations in terms of environmental variables is available in Appendix 2. Removing stations for the RDA reduced the total number of taxa found at least at two stations from 303 to 266. The RDA was performed after Hellinger transformation to reduce the importance of dominant taxa (Legendre & Gallagher 2001). Environmental variables entered into the model were: seven food supply proxies (polynya presence/absence, PP 5Y and PP 1Y, sediment organic carbon, sediment phaeopigments, sediment Chl *a*, and euphotic B_T), five direct variables (three bottom oceanographic variables (bottom oxygen, salinity and temperature), substrate type, sediment $\delta^{13}C$), and three indirect/spatial variables (depth, latitude, longitude). We performed two RDA: one included variables from all types of environmental categories and the other excluded indirect/spatial variables because the latter may mask food supply and direct gradients that have higher ecological significance (McArthur *et al.* 2010). Reduction of explanatory variables was performed by forward selection on the basis of their permutation p values (9999 permutations) and on Akaike's Information Criterion (AIC) in case of ties. Collinearity of significant forward selected explanatory variables was verified looking at variance inflation factors (VIF) < 10 (Quinn & Keough 2002).

Statistical analyses were performed using the statistical package R version 3.0 (R Core Team 2013). Statistical significance at $\alpha < 0.05$ was used for all statistical tests except for Spearman correlations and Kruskal-Wallis post-hoc multiple comparison tests, where a statistical significance at $\alpha < 0.01$ was used to account for the increasing probability of type I error in multiple testing (Quinn & Keough 2002). The distribution of biomass, density, $S_{density}$ and H' were mapped with ArcGIS 9.3.1 with color bins defined by the Jenks iterative method which minimizes within class difference and maximizes between class differences (Jenks & Caspall 1971).

RESULTS

Community characteristics: biological and environmental linkages

A total of 527 unique taxa were identified at the lowest possible taxonomic level across all 78 stations (430 at the species level). Faunal biomass across all stations ranged from < 1 to 77 g m^{-2}, density from < 1 to 382 ind. m^{-2}, $S_{density}$ from 16 to 374 taxa 1000 m^{-2}, H' from 0.48 to 3.21, J' from 0.16 to 0.85, and Δ^* from 71.8 to 99.4 (Figure 14). Distribution of benthic biomass, density, $S_{density}$ and H' showed some distinct spatial patterns (Figure 14); J' and Δ^* were not mapped due to their poor association with environmental gradients. Density, biomass and $S_{density}$ were positively correlated with each other, as were H' and J' (Table 5). Biomass and J' were negatively correlated, and Δ^* was not correlated with any community characteristics and also with no environmental variables.

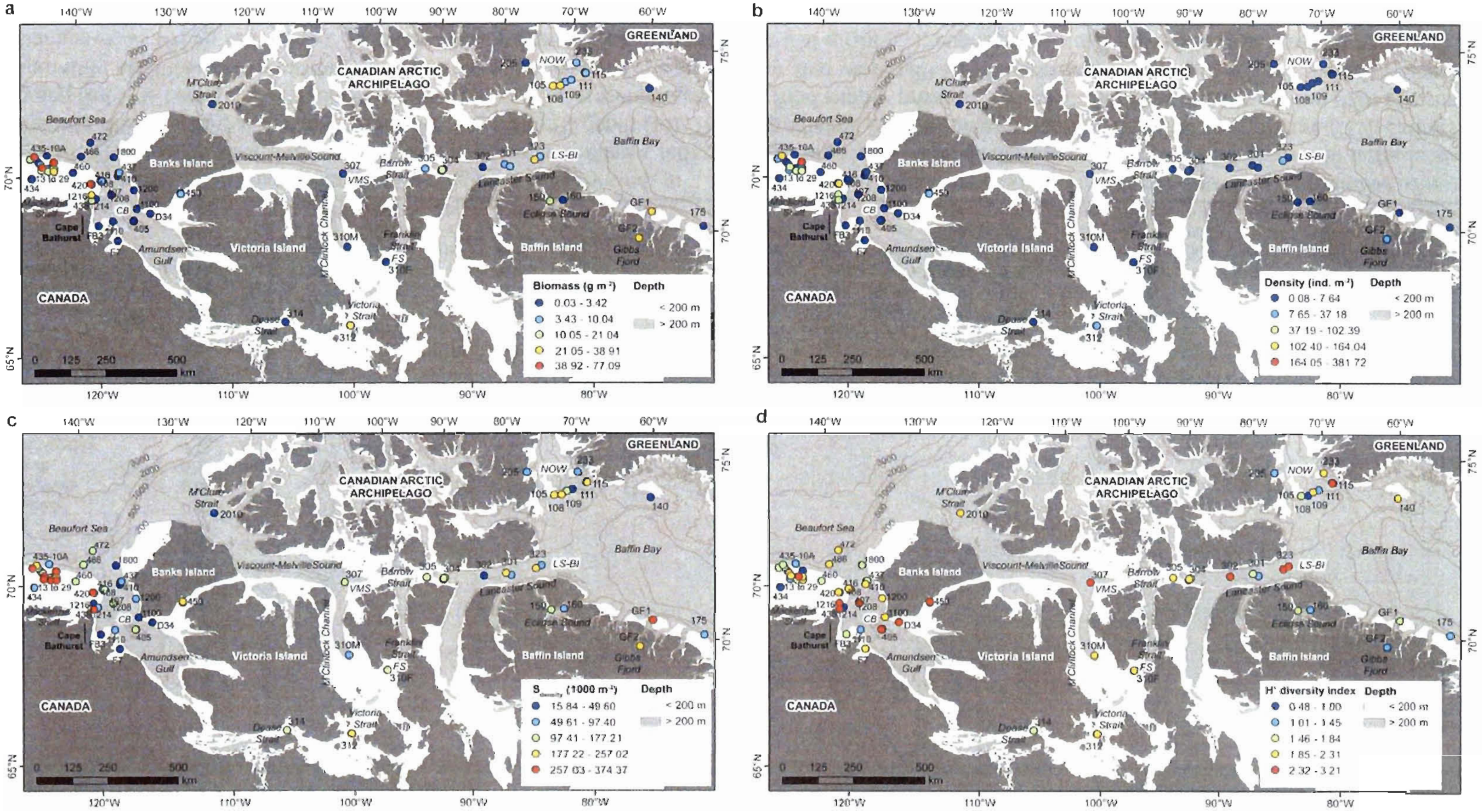

Figure 14. Distributions of benthic community characteristics at 78 stations over 2007-2011. (**a**) biomass (g m^{-2}); (**b**) density (ind. m^{-2}); (**c**) $S_{density}$ (no. of taxa 1000 m^{-2}); (**d**) Shannon-Wiener's diversity index (H').

Table 5. Spearman rank correlation coefficients for relationships between benthic univariate community characteristics and environmental variables. Significant correlations ($p < 0.01$) are indicated in **bold**.

Spatial variability	Meso to large scale (in continental-scale study)						Large scale (100-1000 km)							Meso scale (10-100 km)							
Temporal variability	Years to decades						Relatively stable			Low (> 10 years)			Medium (1-10 years)				High (seasonal)				
Variable type	Benthic community characteristic						Indirect/spatial gradient			Direct gradient				Resource gradient/food supply proxy							
	Biomass	Density	$S_{density}$	H'	J'	Δ*	Latitude	Longitude	Depth	Temperature	Salinity	Oxygen	Sed. $\delta^{13}C$	Sed. OC	PP 5Y	PP 1Y	Sed. phaeo	Sed. Chl *a*	Euphotic B_T	Euphotic B_S	Euphotic B_L
Biomass	1.00																				
Density	**0.84**	1.00																			
$S_{density}$	**0.64**	**0.73**	1.00																		
H'	-0.05	0.20	**0.30**	1.00																	
J'	**-0.40**	-0.15	-0.20	**0.79**	1.00																
Δ*	-0.11	-0.07	0.00	-0.12	-0.05	1.00															
Latitude	0.07	-0.11	-0.11	**-0.44**	**-0.35**	-0.06	1.00														
Longitude	0.01	-0.16	-0.07	-0.27	-0.16	0.04	**0.57**	1.00													
Depth	-0.25	**-0.34**	-0.26	**-0.39**	-0.20	-0.02	**0.66**	**0.65**	1.00												
Temperature	-0.12	-0.19	-0.18	**-0.37**	-0.19	-0.11	**0.46**	**0.46**	**0.76**	1.00											
Salinity	**-0.38**	**-0.44**	**-0.51**	**-0.45**	-0.11	-0.04	**0.47**	0.29	**0.79**	**0.71**	1.00										
Oxygen	0.22	**0.30**	**0.43**	**0.38**	0.08	0.02	**-0.50**	**-0.55**	**-0.67**	**-0.61**	**-0.65**	1.00									
Sed. $\delta^{13}C$	-0.06	-0.25	-0.25	-0.28	-0.20	0.03	**0.59**	**0.76**	**0.60**	**0.37**	**0.37**	**-0.55**	1.00								
Sed. OC	0.01	0.00	-0.02	0.15	0.12	-0.01	0.26	-0.09	0.16	0.12	0.15	-0.17	0.06	1.00							
PP 5Y	**0.45**	**0.38**	0.26	0.16	-0.01	-0.10	-0.07	-0.30	nr	nr	nr	nr	-0.31	**0.57**	1.00						
PP 1Y	**0.44**	**0.35**	0.30	0.20	-0.01	-0.22	-0.07	-0.30	nr	nr	nr	nr	-0.29	**0.51**	**0.92**	1.00					
Sed. phaeo	0.25	0.17	0.09	0.17	0.05	0.02	0.24	0.10	-0.01	-0.08	-0.19	-0.06	0.17	**0.65**	**0.56**	**0.44**	1.00				
Sed Chl *a*	**0.36**	0.31	0.25	0.28	0.05	-0.08	-0.03	-0.15	**-0.38**	-0.33	**-0.54**	0.28	0.03	**0.51**	**0.58**	**0.55**	**0.80**	1.00			
Euphotic B_T	-0.18	-0.21	-0.15	-0.20	-0.15	-0.04	0.17	**0.45**	nr	nr	nr	nr	**0.61**	-0.18	**-0.35**	**-0.40**	-0.03	-0.12	1.00		
Euphotic B_S	-0.12	-0.07	0.06	-0.04	-0.08	-0.06	-0.12	0.05	nr	nr	nr	nr	-0.10	-0.06	-0.24	-0.31	-0.21	-0.31	**0.55**	1.00	
Euphotic B_L	0.18	0.13	0.10	-0.03	-0.19	-0.12	0.13	0.24	nr	nr	nr	nr	**0.55**	0.13	0.07	-0.03	**0.36**	**0.40**	**0.89**	0.21	1.00
Euphotic B_L:B_T	0.28	0.25	0.04	0.06	-0.01	-0.08	0.05	0.10	nr	nr	nr	nr	**0.50**	0.19	0.30	0.24	**0.47**	**0.56**	**0.45**	-0.34	**0.78**

Benthic community characteristics: biomass (g m^{-2}); density (ind. m^{-2}; without colonial organisms); $S_{density}$: taxon richness density (number of taxa m^{-2}); H′: Shannon–Wiener's diversity index; J′: Pielou's evenness index; Δ*: average taxonomic distinctness. Indirect/spatial gradients: latitude and longitude (km; starting at the most southwestern station); depth (m). Direct gradients: Bottom oceanographic variables: temperature (°C); salinity; oxygen (ml l^{-1}). Terrestrial influence: sediment $\delta^{13}C$ (‰). Resource gradients/food supply proxies: sed. OC: sediment organic carbon (%); PP: sum of monthly satellite-derived primary production estimates over one (PP 1Y) or five years (PP 5Y) before sampling (mg C m^{-2} y^{-1}; model results of Bélanger *et al.* 2013); sed. phaeo: sediment phaeopigments (µg g^{-1}); sediment Chl *a* (µg g^{-1}); euphotic B_T: total phytoplankton biomass (cells ≥ 0.7 µm; mg Chl *a* m^{-2}); euphotic B_S: biomass of small phytoplankton cells (0.7–5 µm; mg Chl *a* m^{-2}); euphotic B_L: biomass of large phytoplankton cells (≥ 5 µm; mg Chl *a* m^{-2}); euphotic B_L:B_T : relative contribution of large cells to total biomass. nr: biologically not relevant.

Among the relationships tested with indirect/spatial variables, H' and J' were negatively correlated with latitude (from south to north); density and H' were negatively correlated with depth. Regression models relating benthic biomass, density, $S_{density}$ and H' with depth had poor explanatory power, in part due to the positive influence of the productive LS-BI and NOW polynyas at deep stations (Figure 15). Among the correlations tested with bottom oceanographic variables, H' was negatively correlated with temperature; biomass, density, $S_{density}$ and H' were negatively correlated with salinity; density, $S_{density}$ and H' were positively correlated with oxygen. Among the correlations tested with food supply proxies, biomass and density were positively correlated with PP 1Y and PP 5Y, and biomass was positively correlated with sediment Chl *a* (Table 5). No benthic community characteristic was significantly correlated with sediment $\delta^{13}C$, sediment organic carbon, sediment phaeopigments, or any descriptors of euphotic phytoplankton biomass. Lower $S_{density}$ and H' values were found in hard substrate stations than in soft substrate stations (Table 6). H' was significantly lower at stations located within than outside a polynya (Table 6).

Spatial variables were highly correlated (correlation coefficient > 0.5) with all direct gradient variables (bottom oceanographic variables and sediment $\delta^{13}C$) (Table 5). Sediment Chl *a* was the only sediment food supply proxy correlated negatively with depth. Food supply proxies in surface waters representing different temporal integration of primary productivity varied in opposite directions: integrated PP estimates (PP 5Y and PP 1Y) and seasonal euphotic B_T were negatively correlated. However, food supply proxies in sediment varied in the same direction: sediment organic carbon, sediment phaeopigments and sediment Chl *a* were positively correlated. These latter three sediment food supply proxies also were positively correlated to PP 5Y and PP 1Y; only sediment phaeopigments and sediment Chl *a* were positively correlated to the highly seasonal euphotic B_L and euphotic B_L:B_T (Table 5).

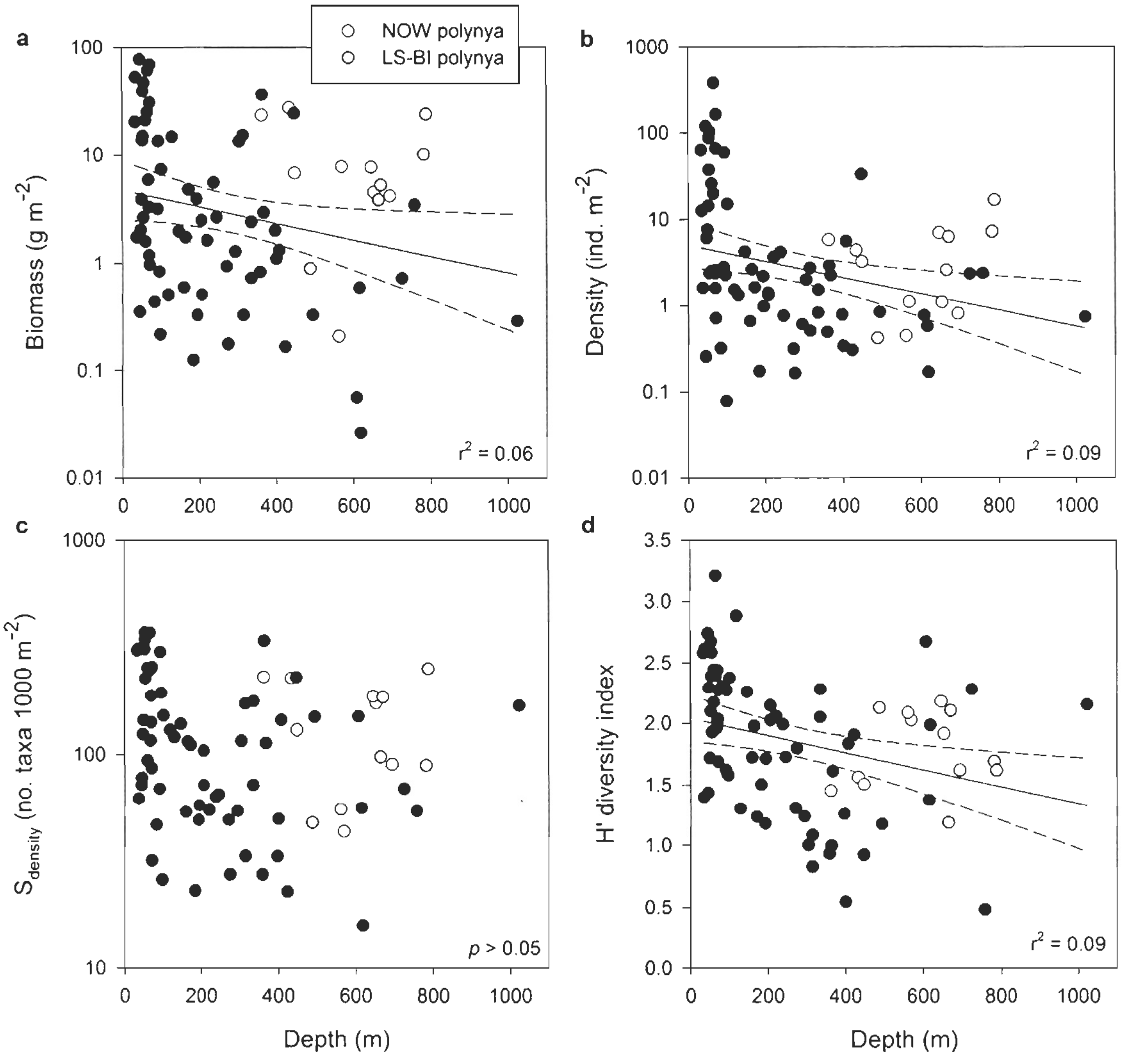

Figure 15. Relationships of benthic community characteristics with depth. Stations sampled underneath Lancaster Sound-Bylot Island polynya (LS-BI; gray circles) and NOW polynya (white circles) are highlighted. (**a**) biomass (g m^{-2}); (**b**) density (ind. m^{-2}); (**c**) Sdensity (no. of taxa 1000 m^{-2}); (**d**) Shannon-Wiener's diversity index (H'). Coefficients of determination of significant linear regressions ($p < 0.05$) are shown and dashed lines represent 95 % confidence intervals.

Table 6. Results of significant differences in benthic community characteristics between environmental categories and among community clusters.

Community characteristic/ Categorical variable	Substrate type (Hard *vs.* Soft)	Polynya (Presence *vs.* Absence)	Community clusters (Fig. 16) (significant differences are shown)
Biomass	ns	ns	Deep coldspots < Local hotspots; Shelf break < Local hotspots; Deep coldspots < Mackenzie Shelf; Shelf break < Mackenzie Shelf
Density	ns	ns	Deep coldspots < Local hotspots; Deep coldspots < Mackenzie Shelf; Shelf break < Mackenzie Shelf
$S_{density}$	Hard < Soft	ns	Deep coldspots < Mackenzie Shelf; Shelf break < Mackenzie Shelf
H'	Hard < Soft	Presence < Absence	Deep coldspots < Mackenzie Shelf; Local hotspots < Mackenzie Shelf
J'	ns	ns	ns
Δ^*	ns	ns	ns

Mann-Whitney *U* tests were applied on categorical variables with two states, while Kruskal-Wallis tests were used to test for difference among community clusters (post-hoc comparisons at $\alpha = 0.01$). ns: non-significant.

Community clusters and distribution patterns

Ward clustering analysis resulted in six well-defined community clusters (Figure 16). We attributed a 'label' to each community cluster based on three variables (mean biomass, mean depth, proportion of hard/soft substrate stations) and their respective minimal and maximal values among clusters (Table 7). The term 'coldspots' was attributed to the community cluster with the lowest mean biomass, and the term 'hotspots' was given to the community cluster characterized by highest mean biomass. Because the 'hotspots' community type was spatially distributed at discrete locations across the study area, we named it 'local hotspots' community. Substrate type (hard or soft) was added to the name of a cluster when almost all, if not all stations, were of one substrate type. The mean depth around the 200 m shelf break was chosen as the main attribute for the 'shelf break' cluster.

Depth was used as a descriptor when all stations were deeper than 200 m (only station 1216 in 'deep soft substrate' cluster was < 200 m, Figure 17). The 'Mackenzie Shelf' community cluster was the only one named based on its geographical location (Figure 17) and was the most dissimilar in terms of taxonomic composition compared with all other clusters (Figure 16). The other five community clusters formed two major groups: one group with two clusters found at deep stations ('deep coldspots' and 'deep soft substrate' clusters) and the second group composed of the remaining three community clusters ('hard substrate', 'shelf break', 'local hotspots') (Figure 16). Across all community clusters, dominant taxa in terms of biomass were often large echinoderms (e.g., sea star, brittle star, basket star, sea cucumber), sea anemones and sponges, but also high biomass of the bivalves *Astarte* spp. and isopods *Saduria* spp. prevailed in some community clusters (Table 7). The distinctiveness of the 'Mackenzie Shelf' taxonomic composition was well represented by the high 'IndVal' index values (≥ 82 %) of the top five significant indicator taxa, meaning that those taxa were almost exclusively found in this community cluster (Table 7). Comparatively, the significant indicator taxa of the other five community clusters had 'IndVal' values between 22 % and 62 % and occurred in more than one community cluster (Table 7). The 'Mackenzie Shelf' community cluster was composed of stations with significantly higher biomass, density and $S_{density}$ than stations in 'deep coldspots' and 'shelf break' clusters, and with higher H' than 'deep coldspots' and 'local hotspots' communities (Table 6). 'Local hotspots' community cluster stations had greater biomass than stations in 'deep coldspots' and 'shelf break' communities, and greater density than 'deep coldspots' cluster stations (Table 6). J' and Δ^* were not significantly different among community clusters (Table 6).

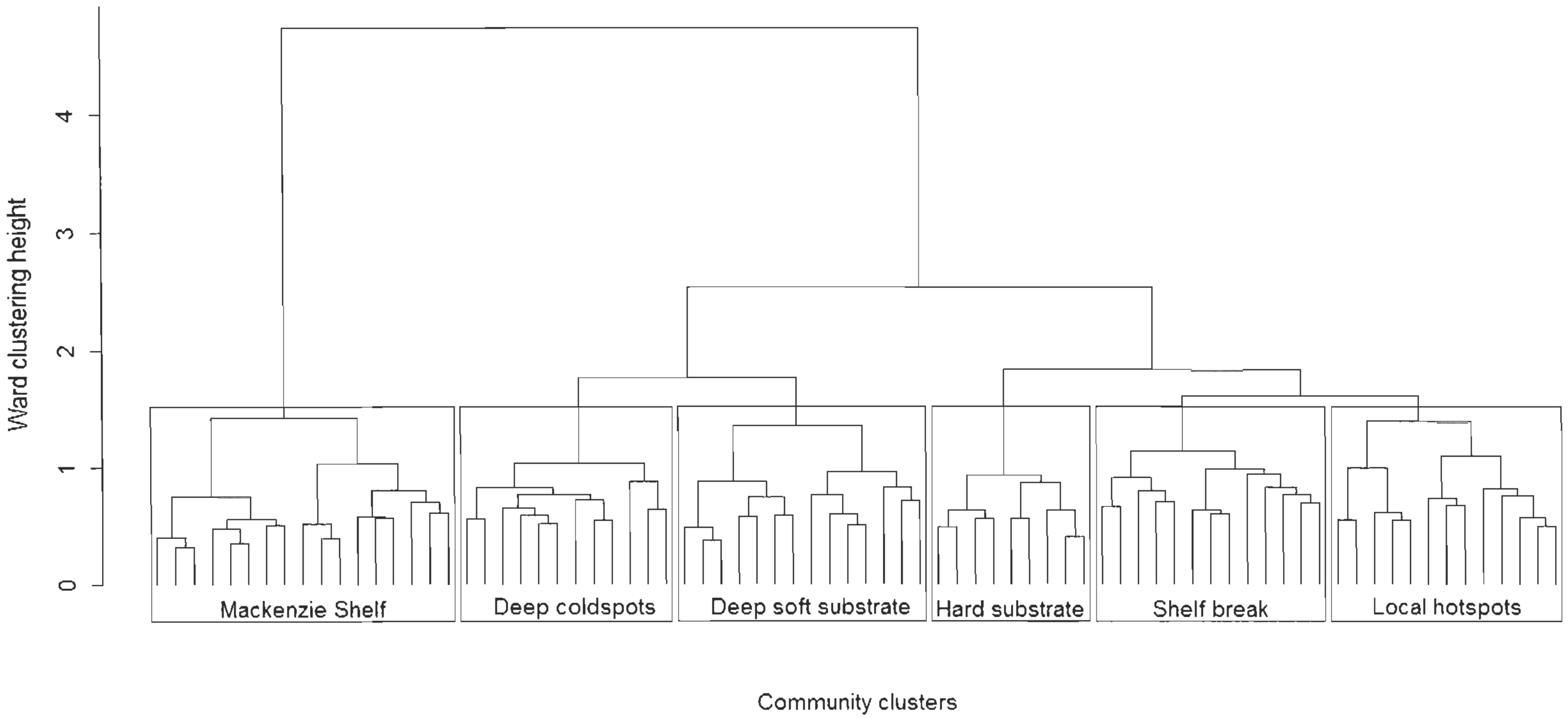

Figure 16. Community cluster partition. Ward's minimum variance cluster analysis based on Bray-Curtis dissimilarity matrix using fourth-root transformed megafaunal biomass data at 78 stations over 2007-2011.

Table 7. Megabenthic community clusters and their respective total taxonomic richness, mean biomass, mean depth, as well as the proportion of hard/soft substrate stations in each cluster (variables used to attribute a 'label' to each community are in **bold**). For each community cluster, the five dominant taxa in terms of biomass and the five most significant indicator taxa ($p < 0.05$) ranked according to their indicator value index (IndVal) are shown.

Community cluster	No. of stations N=78	Total taxonomic richness (range for stations)	Mean biomass (± SD) ($g\ m^{-2}$)	Mean depth (± SD) (m)	Substrate type proportion (hard/soft stations)	Dominant taxa	Fide-lity (%)	Significant indicator taxa -ex aequo are shown-	Specificity (%)	Fidelity (%)	IndVal (%)
Mackenzie Shelf	17	179 (25-119)	18.70 (21.85)	58 (14)	0/17	*Icasterias* sp. (Sea star)	53	*Cistenides* sp. (Polychaete: Pectinariidae)	100	100	100
						Astarte spp. (Bivalve)	65	*Macoma* spp. (Bivalve)	99	100	99
						Saduria spp. (Isopod)	100	*Saduria* spp. (Isopod)	93	100	93
						Gorgonocephalus spp. (Basket star)	29	*Pontoporeia* sp. (Amphipod)	100	88	88
						Ophiocten sp. (Brittle star)	82	*Ciliatocardium* sp. (Bivalve)	93	88	82
Deep coldspots	12	114 (11-52)	**0.73 (0.61)**	**498 (199)**	3/9	*Ophiopleura* sp. (Brittle star)	92	*Bythocaris* sp. (Decapod)	56	75	42
						Ophiacantha sp. (Brittle star)	67	*Amage* sp. (Polychaete: Ampharetidae)	96	33	32
						Pontaster sp. (Sea star)	67	*Siphonodentalium* sp. (Scaphopod)	50	58	29
						Ctenodiscus sp. (Sea star)	17	*Apherusa* sp. (Amphipod), *Sarsiflustra* sp. (Bryozoan)	100	25	25
						Icasterias sp. (Sea star)	25	*Myrioglobula* sp. (Polychaete: Oweniidae)	98	25	24
Deep soft substrate	14	126 (11-64)	6.96 (9.09)	**485 (261)**	**1/13**	*Gorgonocephalus* spp. (Basket star)	14	*Pontaster* sp. (Sea star)	60	79	47
						Astarte spp. (Bivalve)	100	*Psilaster* sp. (Sea star)	100	43	43
						Actinauge sp. (Anemone)	29	*Asychis* sp. (Polychaete: Maldanidae)	98	43	42
						Psolus sp. (Sea cucumber)	7	Zoanthidae (Zoanthid)	95	43	41
						Ophiopleura sp. (Brittle star)	79	*Scalpellum* sp. (Barnacle)	100	36	36

Table 7 continued.

Community cluster	No. of stations N=78	Total taxonomic richness (range for stations)	Mean biomass (± SD) ($g\ m^{-2}$)	Mean depth (± SD) (m)	Substrate type proportion (hard/soft stations)	Dominant taxa	Fidelity (%)	Significant indicator taxa -ex aequo are shown-	Specificity (%)	Fidelity (%)	IndVal (%)
Hard substrate	9	125 (22-60)	8.11 (11.30)	289 (179)	**9/0**	Porifera (Sponges)	67	Porifera (Sponges)	93	67	62
						Strongylocentrotus sp. (Urchin)	100	*Ophiacantha* sp. (Ophiuroid)	49	100	49
						Actinauge sp. (Anemone)	33	*Ophiopus* sp. (Ophiuroid)	69	44	31
						Gorgonocephalus spp. (Basket star)	56	*Strongylocentrotus* sp. (Urchin)	29	100	29
						Ophiacantha sp. (Brittle star)	100	*Eurycyde* sp. (Pycnogonid), *Glycera* sp. (Polychaete: Glyceridae), *Halice* sp. (Amphipod)	100	22	22
Shelf break	13	140 (10-63)	1.35 (2.02)	**180 (92)**	3/10	*Ophiocten* sp. (Brittle star)	85	*Yoldiella* spp. (Bivalve)	78	46	36
						Urasterias sp. (Sea star)	15	*Laonice* sp. (Polychaete: Spionidae)	85	31	26
						Hyas sp. (Crab)	8	-	-	-	-
						Nuculana spp. (Bivalve)	46	-	-	-	-
						Saduria spp. (Isopod)	15	-	-	-	-
Local hotspots	13	206 (15-86)	**21.54 (21.82)**	301 (233)	3/10	*Gorgonocephalus* spp. (Basket star)	38	Nephtheidae (Soft corals)	61	92	56
						Dendrochirotida (Sea cucumber)	38	*Phascolion* sp. (Sipuncula: Phascolionidae)	91	54	49
						Balanus sp. (Barnacle)	23	*Buccinum* spp. (Gastropod)	79	62	49
						Strongylocentrotus sp. (Urchin)	23	*Nymphon* spp. (Pycnogonid)	59	77	45
						Ophiopleura sp. (Brittle star)	38	*Eualus* spp. (Decapod)	73	54	39

SD: standard deviation. 'IndVal' index is a measure of association between a taxon and a cluster of sites and is calculated as the product of specificity (mean biomass of a given taxon within a cluster compared to the other clusters) and fidelity (taxon occurrence at sites belonging to a cluster)

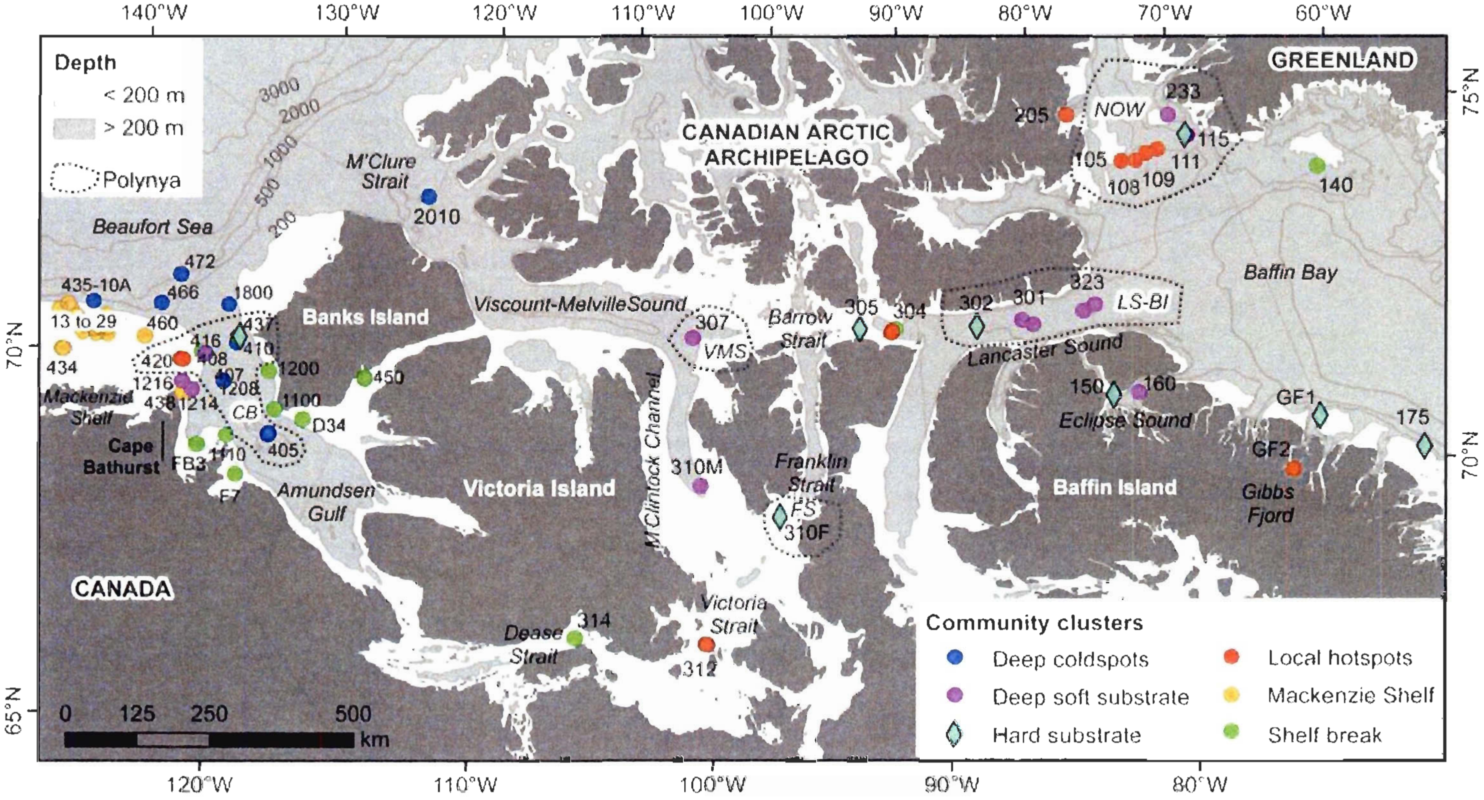

Figure 17. Locations of the six megabenthic community clusters.

Relative mean biomass contribution of the main phyla and cumulative total biomass varied between community clusters (Figure 18). The 'Mackenzie Shelf' community cluster was characterized by high biomass of Echinodermata (43 %) and Bivalvia (28 %). Echinodermata dominated biomass (76 %; mostly Ophiuroidea) at almost all stations of the 'deep coldspots' cluster. Biomass of Echinodermata (47 %; almost equally Asteroidea, Crinoidea, Holothuroidea and Ophiuroidea), Bivalvia (27 %) and Cnidaria (17 %; mostly Anthozoa) were high at several stations of the 'deep soft substrate' cluster. For stations of the 'hard substrate' cluster, Porifera (65 %) and Echinodermata (23 %; mostly Echinoidea) were dominating biomass. 'Shelf break' and 'local hotspots' clusters were similar in relative biomass with high Echinodermata biomass (43-62 %; both having predominantly high biomass of Echinoidea, but successively high biomass of Holothuroidea for 'local hotspots' and high biomass of Asteroidea and Ophiuroidea for 'shelf break'), and high biomass of Arthropoda (14-22 %) and Mollusca (15-16 %). A station-based account of the relative contribution of the main phyla for biomass and taxonomic richness is available in Appendix 2.

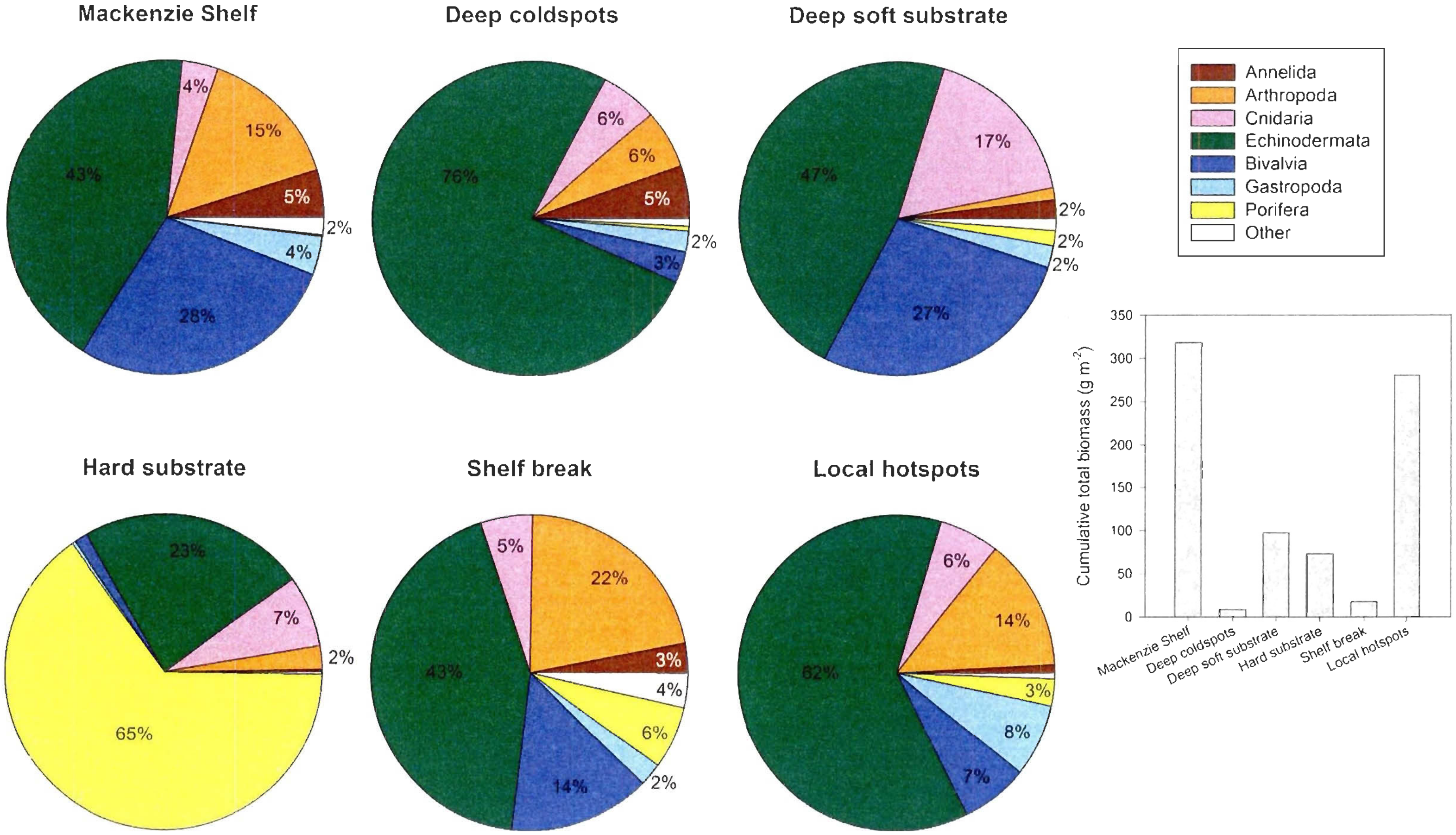

Figure 18. Variation in mean relative biomass composition (%; only ≥ 2 % shown) for the main phyla or classes sampled in all community clusters (pie charts) and cumulative total biomass (g m^{-2}) sampled per community cluster (histogram).

Environmental drivers of community clusters

Community clusters were significantly influenced by a set of environmental variables that explained between 19 % and 22 % ($R^2_{adjusted}$) of the variation in the RDA analysis. These are low but typical variance levels explained for biological systems (Cottenie 2005), as the high complexity of these systems rarely makes it conceivable to encompass all the variables that balance the responses of organisms or communities (Moller & Jennions 2002). Among the fifteen explanatory variables (including indirect/spatial variables) employed in the forward selection of the RDA model on 50 stations, seven variables were retained (Table 8, Figure 19a). The final model significantly explained 22 % of the taxonomic composition variation (R^2 = 0.33, R^2_{adj} = 0.22). Depth, longitude, latitude, sediment Chl *a* and bottom oxygen were strongly correlated with the first RDA axis, while substrate type and sediment organic carbon were highly correlated with the second RDA axis (Table 8, Figure 19a). Among the twelve explanatory variables included in the forward selection of the RDA model excluding indirect/spatial variables, six were retained (Table 8, Figure 19b). The final model significantly explained 19 % of the mega-epibenthic taxonomic composition variation (R^2 = 0.29, R^2_{adj} = 0.19). Bottom salinity, oxygen, temperature and sediment $\delta^{13}C$ were strongly correlated with the first RDA axis, while substrate type and sediment organic carbon were highly correlated with the second RDA axis (Table 8, Figure 19b). The first RDA axes of both models reflected mostly the distribution of community clusters along two large-scale environmental gradients (100-1000 km): (1) a vertical gradient created by depth, bottom oceanographic variables and sediment Chl *a* variables, and (2) a geographical gradient generated by longitude, latitude and sediment $\delta^{13}C$ variables. The second RDA axes of the models reflected the distribution of community clusters along a meso-scale environmental gradient (10-100 km) of the sedimentary environment characterized by the variables substrate type and sediment organic carbon. The six community clusters obtained from the unconstrained Ward clustering analysis (Figure 16) were well segregated within the RDA models, except the 'local hotspots' community cluster with stations scattered along the second RDA axes. The sediment organic carbon content recorded within this community was highly variable, from high values underneath NOW polynya and in Barrow Strait to low values in Victoria Strait and off Cape Bathurst.

Table 8. Redundancy analysis (RDA) results on relationships between megabenthic biomass-based taxonomic composition and environmental variables for a subset of 50 sites sampled from 2008 to 2011. Two RDA analyses were performed, with and without spatial variables, and both were significant ($p < 0.001$; 9999 permutations). Results from the first two RDA axes are shown and environmental variables are listed in order following forward selection (9999 permutations).

With spatial variables			Without spatial variables		
	RDA axis 1	RDA axis 2		RDA axis 1	RDA axis 2
Eigenvalue	0.09	0.07	Eigenvalue	0.09	0.06
Variance explained	0.35	0.26	Variance explained	0.37	0.27
Correlations with environmental variables			Correlations with environmental variables		
Depth	0.95	0.18	Bottom temperature	0.82	-0.24
Substrate (hard)	-0.02	-0.63	Substrate (hard)	0.11	0.66
Substrate (soft)	0.00	0.14	Substrate (soft)	-0.02	-0.14
Longitude	0.67	-0.49	Sediment $\delta^{13}C$	0.79	0.18
Latitude	0.61	-0.01	Bottom salinity	0.75	-0.29
Sediment Chl *a*	-0.42	0.24	Sediment organic carbon	-0.08	-0.74
Sediment organic carbon	0.03	0.66	Bottom oxygen	-0.73	0.20
Bottom oxygen	-0.70	0.03			

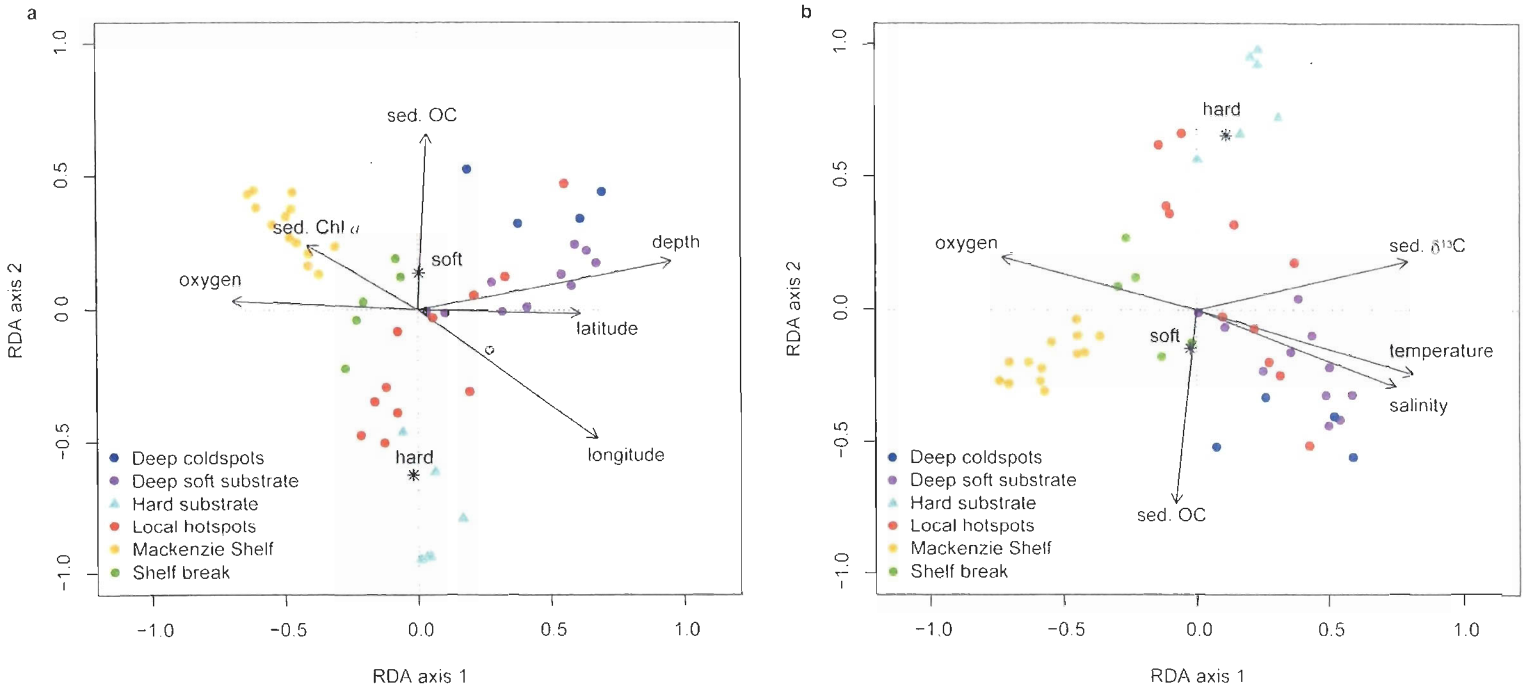

Figure 19. Redundancy analysis (RDA) ordination plots of megabenthic biomass-based taxonomic composition against forward selected environmental variables (black arrows and centroids) on 50 stations from 2008 to 2011. (**a**) Including indirect/spatial variables; the first two RDA axes explained 61 % of the variance. (**b**) Without spatial variables; the first two RDA axes explained 64 % of the variance. The categorical variable 'substrate type' is illustrated using centroids for each category (hard and soft) and colors represent the six benthic communities defined in this study.

DISCUSSION

This study represents the first continental-scale assessment of the taxonomic composition of megabenthic communities and the relationships of various environmental factors acting at different spatial and temporal scales to their community structure. As we hypothesized, benthic univariate community characteristics had a tendency to decrease with depth and increase with food supply proxies, but few correlations were significant. Distribution patterns of community clusters were significantly associated with large- and meso-scale environmental factors, but again explanatory power of the models was moderate. We discuss how local- to meso-scale environmental conditions in specific locations of the Canadian Arctic disrupt the hypothetical large-scale trends we expected to observe with depth and food supply proxies. We conclude that broad generalizations based on these community-environment relationships over the large geographical extent of the Canadian Arctic are not straightforward unless predictions take into account the influence of local- to meso-scale environmental conditions at some locations.

Environmental drivers of community structure

We propose a conceptual model illustrating spatial and temporal scales of variability of the significantly retained environmental drivers of megabenthic community characteristics and cluster distribution (Figure 20). All direct and indirect/spatial gradient variables considered were significantly related to community characteristics and/or cluster distribution. Among several food supply proxies tested, four were significantly retained, i.e., sediment Chl *a*, sediment organic carbon, PP 1Y and PP 5Y. We refer to this conceptual model in the discussion below.

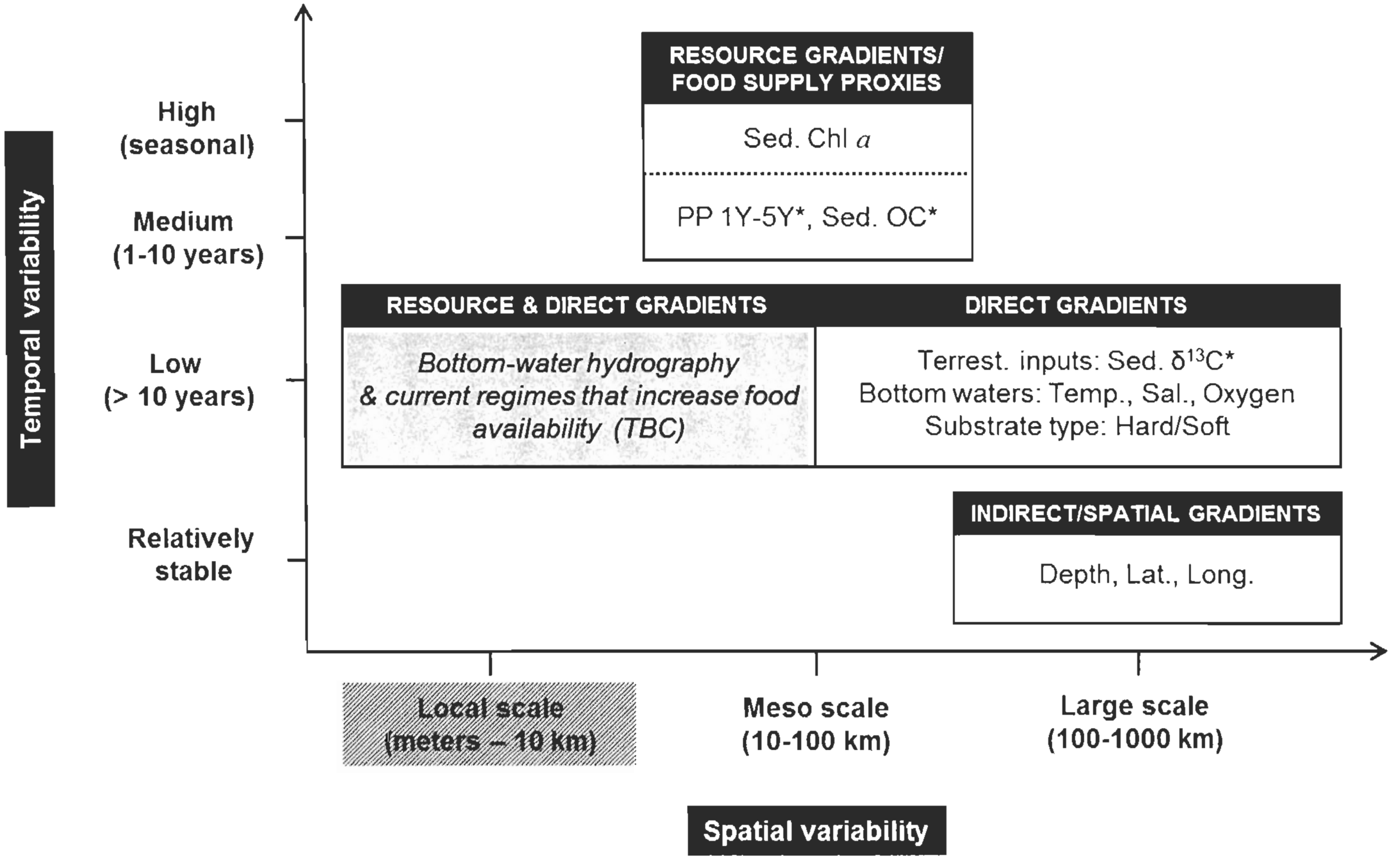

Figure 20. Conceptual figure displaying the overall results of environmental drivers of megabenthic communities in this study in relation to their spatial and temporal scales of variability; potential missing important drivers (gray box) would have to be confirmed (TBC). Environmental factors available for the present study were divided into three categories: resource, direct and indirect/spatial gradients (following McArthur *et al.* 2010). Sampling design of the present study prevented conclusion at local scale (dashed). * denotes environmental variables that were either significantly correlated with univariate community characteristics or to community cluster distribution.

Large-scale environmental gradients

The decrease of benthic biomass and density with depth in the World's oceans in general (e.g., Levin *et al.* 2001; Rex *et al.* 2006; Wei *et al.* 2012), and in Arctic systems specifically (e.g., Curtis 1975; Thomson 1982; Mayer & Piepenburg 1996; Jones *et al.* 2007; Bluhm *et al.* 2011a), has been commonly acknowledged to be a reflection of the vertical decline of organic material flux reaching the seafloor (Suess 1980; Carmack & Wassmann 2006). This link to declining food deposition can be seen in the present study by the negative correlation between sediment Chl *a* and depth. The positive correlation we found between sediment Chl *a* and the absolute amount as well as the relative proportion of large phytoplankton cells (≥ 5 μm) support the fact that large, rapidly-sinking cells contribute most to the carbon flux reaching the seafloor (Wassmann 1998). The parallel significant declines of sediment Chl *a* and benthic biomass with depth support that deep communities sampled in this study were likely constrained by the supply of fresh organic matter. The strength of the correlations was, however, only moderate (correlation coefficients < 0.5), meaning that the assumption of decreasing food supply, benthic biomass and density with depth is not necessarily straightforward for the entire Canadian Arctic. The weak decreasing trend of benthic biomass and density with depth over the study area is mostly driven by several biomass-rich and density-rich deep stations (> 200 m) located in the Lancaster Sound-Bylot Island (LS-BI) and NOW polynyas. The strong pelagic-benthic coupling in deep areas of the Eastern Canadian Arctic relative to weak pelagic-benthic coupling in deep areas of the Western Canadian Arctic has also been observed by the spatial variability in the magnitude of benthic boundary fluxes (Link *et al.* 2013b).

In addition to biomass and density, biodiversity metrics (i.e., $S_{density}$ and H') also varied or had a tendency to vary with depth in our study. Depth was strongly linked to physical properties of water masses (salinity, temperature, oxygen) and it is possible that the vertical Pacific/Atlantic water mass gradient may explain in part, beside declining food supply with depth, the depth-related gradients in benthic biodiversity metrics and taxonomic composition. Possible factors, alone or in combination, associated with distinct water masses and that may contribute to benthic diversity patterns include: Influence of physical discontinuities in the water column on distributional patterns of invertebrate larvae (Metaxas 2001); physiological tolerances of benthic organisms to hydrographic conditions (Levin *et al.* 2001); and the geological history such as post-glaciation events that promoted the colonization of American Arctic shelves by species from the Pacific and Atlantic oceans (Dunton 1992). We cannot tease apart the relative influence of these factors or the influence of depth versus water mass, but our results convincingly demonstrated that the two 'deep' community clusters were taxonomically more similar than with shallower community clusters. Bottom oceanographic variables also largely structure benthic communities in other Arctic regions, such as the East Greenland shelf and slope (Mayer & Piepenburg 1996; Piepenburg *et al.* 1997), the northeastern Chukchi Sea (Blanchard *et al.* 2013a; Ravelo *et al.* 2013), and in the Barents Sea (Carroll *et al.* 2008; Cochrane *et al.* 2009; Carroll & Ambrose 2012). Decline in biodiversity with depth also may in part be explained by decreasing availability of fresh food with depth, similar to biomass and density. For example, as food supply decreases, richness may decrease because fewer species can maintain viable populations (Levin *et al.* 2001). We did not, however, find significant correlations either between primary productivity proxies in surface waters and benthic biodiversity metrics or between sediment food supply proxies and benthic biodiversity metrics, making this link likely less important than the control of physical properties of bottom waters.

The sediment $\delta^{13}C$ gradient replaced the spatial variable longitude when the latter was excluded from the RDA model, revealing the influence of terrestrial organic matter inputs on taxonomic composition. Sediment $\delta^{13}C$ exposed a large-scale geographical gradient in taxonomic composition with the majority of communities under terrestrial influence located in the western Canadian Arctic near the Mackenzie River drainage ('Mackenzie Shelf' cluster) or in the coastal/shelf region of the Amundsen Gulf ('shelf break' cluster). The decrease of the contribution of terrigenous organic matter towards the eastern Canadian Arctic has been also documented by various sedimentary biomarkers

(Goni *et al.* 2013). The refractory proportion of allochthonous organic carbon delivered by Arctic rivers is high (Kuzyk *et al.* 2009) and terrestrially-derived carbon is typically of low food quality for marine consumers (Klages *et al.* 2004). The lack of correlations between sediment $\delta^{13}C$ and total benthic biomass and density, and the high benthic biomass observed on the Mackenzie Shelf, however, do not support this effect of low food quality. Therefore, in the present context bulk sediment $\delta^{13}C$ did not indicate on the whole what benthic organisms were consuming and was correctly defined as not relevant in the resource gradients. Possibly, effects of terrestrial influence differ by species or feeding type, thus influencing taxonomic composition but not bulk biomass or density.

Meso-scale environmental gradients

Highly biologically productive areas, such as polynyas, are generally thought to favor benthic systems (Grebmeier & Barry 1991; Ambrose & Renaud 1995). Across the Canadian Arctic, the presence of polynyas was not reflected on the benthos by a change in community structure in this study, with the exception of the LS-BI and NOW polynyas. Variation in primary productivity (in magnitude and composition) and in zooplankton grazing pressure among the Canadian Arctic polynyas likely result in variable carbon supply to the benthos, precluding generalizations. In this study we considered the influence of polynyas only for those stations located directly underneath, but these meso-scale oceanographic features also may have a significant influence on benthic community structure in surrounding areas because of the advective transport of organic material by currents (Grebmeier & Cooper 1995). We were not able to assess the marginal effects of polynyas in this study (e.g., by means of particle interceptor traps) and the great water depths (> 200 m) underneath the polynyas may have enhanced the advection of POC. This would be supported by the higher sediment Chl *a* concentrations found in absence than presence of polynyas in this study (results not shown), but this pattern may again be confounded by the shallower depth of non-polynya stations.

Bulk benthic biomass and density were significantly correlated with 1-year and 5-year integrated PP estimates in surface waters, but not with *in situ* measurements of euphotic phytoplankton biomass, possibly due to the mismatch between a short-term estimate of the primary productivity and its export and the integrated, long-term benthic community responses. Among the few benthic studies in the Arctic using integrated PP estimates as a food supply proxy, a positive correlation has been established for macrofaunal density (Carroll *et al.* 2008; Cochrane *et al.* 2009) in the Barents Sea where seasonal food freshness indicators on the seafloor, such as sediment Chl *a*, were also positively correlated with macrobenthic biomass and density (Carroll *et al.* 2008; Cochrane *et al.* 2009; Carroll & Ambrose 2012; Søreide *et al.* 2013). PP estimates did not, however, significantly explain the taxonomic composition variation of megabenthic communities in the present study, contrary to what was observed for macrobenthic communities in the Barents Sea (Cochrane *et al.* 2009). While sediment organic carbon and sediment phaeopigments have often been significantly correlated with macrobenthic biomass, density, species richness and Shannon-Wiener's diversity (Grebmeier *et al.* 1989; Grebmeier *et al.* 2006; Carroll *et al.* 2008; Carroll & Ambrose 2012), they have typically not been related to megafaunal community characteristics and taxonomic composition (Piepenburg *et al.* 1997; Bluhm *et al.* 2009; Bergmann *et al.* 2011), and also not in this study. Sediment organic carbon contains large fractions of refractory material (Magen *et al.* 2010) and, along with sediment phaeopigments, reflects mid- to long-term organic matter inputs to the seafloor, thus likely representing unattractive organic matter sources. Settlement of fresh material, as seen by the positive influence of sediment Chl *a* on bulk biomass, may be critical for Arctic megabenthic communities, possibly because of the substantial metabolic energy required on an individual basis by large organisms (Rex *et al.* 2006). One missing but highly relevant organic matter source that we could not approximate in the present study is the organic matter pool derived from sea-ice algal communities. Arctic benthic communities may rely heavily on this food source (McMahon *et al.* 2006) and it thus may explain the limited correlation of the primary productivity estimates in open waters in the present study with benthic community structure. We did not have any direct measures of sea ice algae and the complexity of environmental constraints on sea-ice algal biomass (e.g., ice thickness, snow cover, nutrient concentrations; Rozanska *et al.* 2009) did not allow us to estimate export of ice algal biomass from proxies. However, the presence of IP_{25}, an ice algal biomarker, in the surface sediment of seven stations occupied across the study area documents that ice algal export occurred in the study region (Belt *et al.* 2013).

Hard substrates in this study had lower $S_{density}$ and H' than soft substrates, although they generally provide higher habitat complexity than soft substrates and thus tend to house a larger number of species (Buhl-Mortensen *et al.* 2012). This negative relationship of hard substrate bottom on biodiversity may be due to the low number of hard substrate stations sampled in this study and also because organisms were heavily damaged by rocks during trawling, thereby making taxonomic determination arduous. Substrate type, however, significantly explained the variation of taxonomic composition, as also demonstrated in other Arctic studies (Mayer & Piepenburg 1996; Bluhm *et al.* 2009). We propose that, in the context of the present study, substrate type along with sediment organic carbon were mostly indicative of the meso-scale sedimentary environment variability on the second RDA axes with higher deposition of organic carbon in soft substrate than in hard substrate bottoms (see the opposite direction of hard substrate and sediment organic carbon, Figure 19). Sediment organic carbon and substrate variability can be indirect indicators of current transport and sedimentation zones, thus influencing the type of benthic fauna occupying a region (Grebmeier *et al.* 2006). These two environmental factors did not, however, explain well the local- to meso-scale conditions of the sedimentary environment in the 'local hotspots' community type, with stations of this community scattered along the second RDA axes. It is likely that other, unmeasured environmental factors, such as water currents and bottom topography, could explain the distribution of the 'local hotspots' community (Figure 20, also see below).

Distribution patterns of community clusters

The majority of the community clusters were observed throughout the extent of the study area, except 'Mackenzie Shelf' and 'deep coldspots' community clusters, which were restricted to the western Canadian Arctic. A similar geographic segregation was previously observed for the zoogeography of marine bivalves of the Canadian Arctic waters (Lubinsky 1972), confirming an important zoogeographic boundary in the western sector of the Canadian Archipelago between the faunas of the Atlantic and the Pacific sectors. The presence of an independent evolutionary trend in this region caused by Pleistocene isolation, along with the narrow, abrupt shelf of the western Archipelago and the zone of brackish waters at the mouth of the Mackenzie River are all potential barriers to faunistic interchange (Lubinsky 1972). This likely shaped, albeit to an unknown degree, the west-to-east variation in taxonomic composition observed in this study.

'Mackenzie Shelf' community

Community structure in this cluster was most dissimilar to all other clusters, with indicator taxa that were almost exclusively restricted to it. This high faunal distinctiveness is conceivably related to the high terrestrial carbon and freshwater influxes from the Mackenzie River and to the shallow depth range of this community cluster. Among the indicator taxa identified in this community type, the isopod *Saduria* spp., is euryhaline (Hagerman & Szaniawska 1988) and the two indicator bivalve taxa, *Ciliatocardium* sp. and *Macoma* spp., are specific to shallow waters of Arctic shelf areas (Lubinsky 1972). The high specificity and fidelity of these indicator taxa to this community reflected the strong influence by the Mackenzie River. The particular environmental forcing exerted on Arctic benthic community composition by large river inflow geographically is known to structure macrofaunal community distribution patterns (Jørgensen *et al.* 1999; Denisenko *et al.* 2003; Schmid *et al.* 2006; Cusson *et al.* 2007; Conlan *et al.* 2008), and, as we demonstrated here, also megafaunal distribution patterns. The distinct oceanographic, physical and biological properties of large rivers draining onto Arctic shelves create quasi-independent systems, as observed for the Pechora Sea in the southeast Barents Sea (Denisenko *et al.* 2003; Wassmann *et al.* 2006).

'Shelf break' community

This community was found mostly in the Amundsen Gulf region, but also in the Archipelago and in Baffin Bay. The lower benthic biomass and density recorded in this community compared to other community types found at similar depth ranges (i.e., 'local hotspots' and 'hard substrate' clusters) may indicate weaker pelagic-benthic coupling and/or lower food quality as this community was located generally in coastal areas of narrow shelves where terrestrial organic matter inputs were high (as indicated by low sediment $\delta^{13}C$). However, in a parallel study carried out at several stations of this community in Amundsen Gulf region, sediment Chl *a* concentrations and benthic carbon remineralization were above the regional average, indicating relatively tight pelagic-benthic coupling compared to the central Amundsen Gulf region (Darnis *et al.* 2012). The 'shelf break' community was located at a transitional zone between the shelf and the slope but also between the Pacific and the Atlantic water masses, both transitions being around 200 m (McLaughlin *et al.* 2004). The environmental conditions around the shelf break could have generated specific and strong habitat heterogeneity. Physical disturbances may be high for the benthic habitat in coastal areas of the Amundsen Gulf where the narrow shelf is subjected to intense erosion and is influenced to the west by the Mackenzie River sediment load discharge (O'Brien *et al.* 2006). The detrivorous feeding behavior of the two indicator taxa of this community, the bivalve *Yoldiella* spp. and the spionid polychaete *Laonice* sp. (Holte & Gulliksen 1998), supports the notion of high sediment deposition but additional studies are needed to assess the relative influence of either physical discontinuities in the water column or seafloor erosion in shaping this community type.

'Deep coldspots' community

Many stations of this community were located under the CB polynya as well as under a phytoplankton-based eutrophic hotspot defined by Ardyna *et al.* (2011) in the central Amundsen Gulf, revealing the absence of a specific influence of this particular polynya on megafaunal communities. Similarly, this polynya did not influence taxonomic composition of macrofaunal communities (Conlan *et al.* 2008) and low rates of carbon remineralization and benthic boundary fluxes have been measured in this polynya (Forest *et al.* 2011; Darnis *et al.* 2012; Link *et al.* 2013b). It has been proposed recently for the central Amundsen Gulf that the pelagic food web may intercept a major part of the POC before it reaches the seafloor (Forest *et al.* 2011; Sallon *et al.* 2011; Darnis *et al.* 2012), thus dampening the pelagic-benthic coupling in this area. In support of this, high concentrations of degraded pigments were present in surface sediments of the Amundsen Gulf than on the adjacent Mackenzie Shelf (Morata *et al.* 2008).

'Deep soft substrate' community

Contrary to the 'deep coldspots' community, the 'deep soft substrate' community was mostly located in the Eastern Canadian Arctic under the productive NOW and LS-BI polynyas (Ardyna *et al.* 2011; Bélanger *et al.* 2013), where strong pelagic-benthic coupling has been reported (Thomson 1982; Kenchington *et al.* 2011; Darnis *et al.* 2012; Link *et al.* 2013b). While the CB polynya in general does not seem to favor strong pelagic-benthic coupling (see above), the assemblage of several 'deep soft substrate' stations at the western edge of the polynya seems to indicate local- to meso-scale patterns of strong pelagic-benthic coupling at the western polynya margin. Wind-driven upwelling occurs near the CB polynya (Williams & Carmack 2008), which promotes high nutrient replenishment for primary production (Tremblay *et al.* 2011) and strong vertical POC flux (Sallon *et al.* 2011; Forest *et al.* 2013). This high productivity and tight pelagic-benthic coupling is also reflected in the high ampeliscid amphipod biomass in that region (Conlan *et al.* 2013). The large biomass of anemones found at several stations of this community probably reflects regionally specific bottom-water hydrography and/or current regime replenishing their food supply. For instance, strong currents at the eastern deep entrance of Lancaster Sound (Fissel *et al.* 1982) have been acknowledged to maintain high benthic communities of filter feeders (Thomson 1982).

'Hard substrate' community

This community cluster was mostly present in the Eastern Canadian Arctic, but this might be biased by the sampling distribution, as stations with hard substrata were usually avoided. The most significant indicator taxa were suspension feeders, indicative of a strong current regime (Grebmeier & Barry 1991). Not all hard substrate stations were grouped in this community cluster, however, suggesting that a more complete substrate classification would improve our understanding of the influence of substrate variability on taxonomic composition. In landscape-scale studies, terrain variables such as slope and roughness may explain a significant proportion of the community structure variation (Dolan *et al.* 2008; Buhl-Mortensen *et al.* 2012). Unfortunately, habitat descriptions based on videos/images and on acoustic techniques (e.g., multibeam data), including near-bottom flow conditions, are scarce in the Canadian Arctic, and future studies are needed to gain more habitat complexity information.

'Local hotspots' community

The combination of significant environmental drivers retained in the RDA models did not explain well the distribution of the 'local hotspots' community cluster, scattered along the second RDA axes showing a meso-scale gradient (10-100 km) influence of the sedimentary environment. We propose that high biomass and taxonomic similarity among the stations within this cluster may originate from unmeasured local- to meso-scale physical and biological conditions that promoted tight pelagic-benthic coupling and/or lateral advection of suspended particles (Figure 20). In the northeastern Chukchi Sea, it has been recently proposed that macro- and megafaunal community structure are influenced by local-scale topographically-driven water circulation that causes variation in organic carbon deposition (Blanchard & Feder 2013; Blanchard *et al.* 2013b, a). Our data along with previous findings provide supporting evidence for an association between specific bottom-hydrography and/or current regime and the biological characteristics of this community. For instance, soft corals (Nephtheidae) were quasi-omnipresent in this community cluster (in 92 % of stations) and thrive in regions with suspended food particles delivered by strong currents (LaBarbera 1984). In the Eastern Canadian Arctic, for example, the NOW polynya has elevated primary production (Stirling 1997; Klein *et al.* 2002; Tremblay & Smith Jr. 2007), high flux of organic matter (Hamel *et al.* 2002; Hargrave *et al.* 2002; Bailey *et al.* 2013), and high carbon remineralization and benthic boundary fluxes (Kenchington *et al.* 2011; Link *et al.* 2013b) that coincide with a high number of megabenthic 'local hotspots' stations in that region. Moreover, many 'local hotspots' stations were found in the western-central section of the NOW polynya where a strong southward flow of deep, cold water from the Arctic Ocean prevails, while 'deep soft substrate' communities in the deeper eastern section of the polynya were positioned under the weak northward flow of the warmer West Greenland Current (Melling *et al.* 2001), re-emphasizing the influence of hydrographic regime. One 'local hotspot' community was located in the east off Cape Bathurst, where local upwelling (Williams & Carmack 2008) is likely to have caused this one station to have the highest biomass recorded in this study and be the only 'local hotspot' community station in the western sector of the study area. Other 'local hotspots' stations distributed across the study region were not located in areas of high annual pelagic primary production (Bélanger *et al.* 2013) and had low sediment organic carbon values. However, high tidal currents may favor the transport of large amounts of organic matter to the seafloor or resuspension of material, such as in Victoria Strait (station 312, Figure 17) and Barrow Strait (station 304, Figure 17) (McLaughlin *et al.* 2004; Hannah *et al.* 2009). This is in agreement with the high biomass of crinoids, passive suspension feeders (LaBarbera 1984), found in Victoria Strait and the high carbon remineralization rates and benthic boundary fluxes at the 'local hotspot' in Barrow Strait (Kenchington *et al.* 2011; Link *et al.* 2013b). To our knowledge, no information on the current regime exists for the 'local hotspot' station of Gibbs fjord (station GF2, Figure 17). However, this station had a high density of holothurians (*Elpidia* sp.), which have been suggested to be indicative of fresh phytodetritus pulses (Piepenburg *et al.* 1996; Gooday 2002; Bluhm *et al.* 2009; Boetius *et al.* 2013). Our limited understanding of the environmental controls on the 'local hotspots' community defined in this study emphasizes the need to better describe local- to meso-scale bottom-water hydrography and current regimes that could favor high advection of organic material (Figure 20). This is especially true in areas of the central Archipelago where primary productivity is low (Ardyna *et al.* 2011; Bélanger *et al.* 2013), giving rise to the sometimes wrong assumption that food supply for benthic communities would also be low.

SUMMARY AND IMPLICATIONS

The central role of food supply in shaping various benthic community attributes is a central subject of current research in the Arctic as it may be most affected by future climate changes (Bluhm & Gradinger 2008). This study revealed, however, that broad generalization of the pelagic-benthic coupling strength may not always be straightforward, as surface production was not always a good predictor of community structure in our study region across the Canadian Arctic. Depth also was not strongly related to benthic biomass and density over the extent of the Canadian Arctic, likely because meso-scale processes enhanced the food supply for deep benthic communities at some locations, particularly underneath highly productive polynyas. None of the food supply proxies that we included in this study was strongly correlated with benthic community characteristics and taxonomic composition, because none reflected the strength of the pelagic-benthic coupling over the entire geographical extent of the Canadian Arctic. For instance, we argue that low-biomass benthic communities received low food supply in eutrophic areas due to strong pelagic interception of POC fluxes (e.g., CB polynya in the Western Canadian Arctic), while biomass-rich benthic communities were found in oligotrophic areas because of specific local- to meso-scale bottom-water hydrography and/or current regimes likely favoring high advection of organic material (e.g., central Canadian Arctic Archipelago). Local- to meso-scale investigations of water circulation that could influence lateral advection of organic material will improve our ability to understand the environmental controls on Canadian Arctic benthic communities to better understand present patterns, and eventually predict future responses of the Canadian Arctic benthic communities in a changing environment. Finally, the various spatial scales of the environmental gradients influencing benthic communities may benefit the processes of delineating and characterizing Ecologically and

Biologically Significant Areas (EBSAs) (Kenchington *et al.* 2011) within large biogeographic regions of the Canadian Arctic that are primarily based on oceanographic and bathymetric similarities (DFO 2009).

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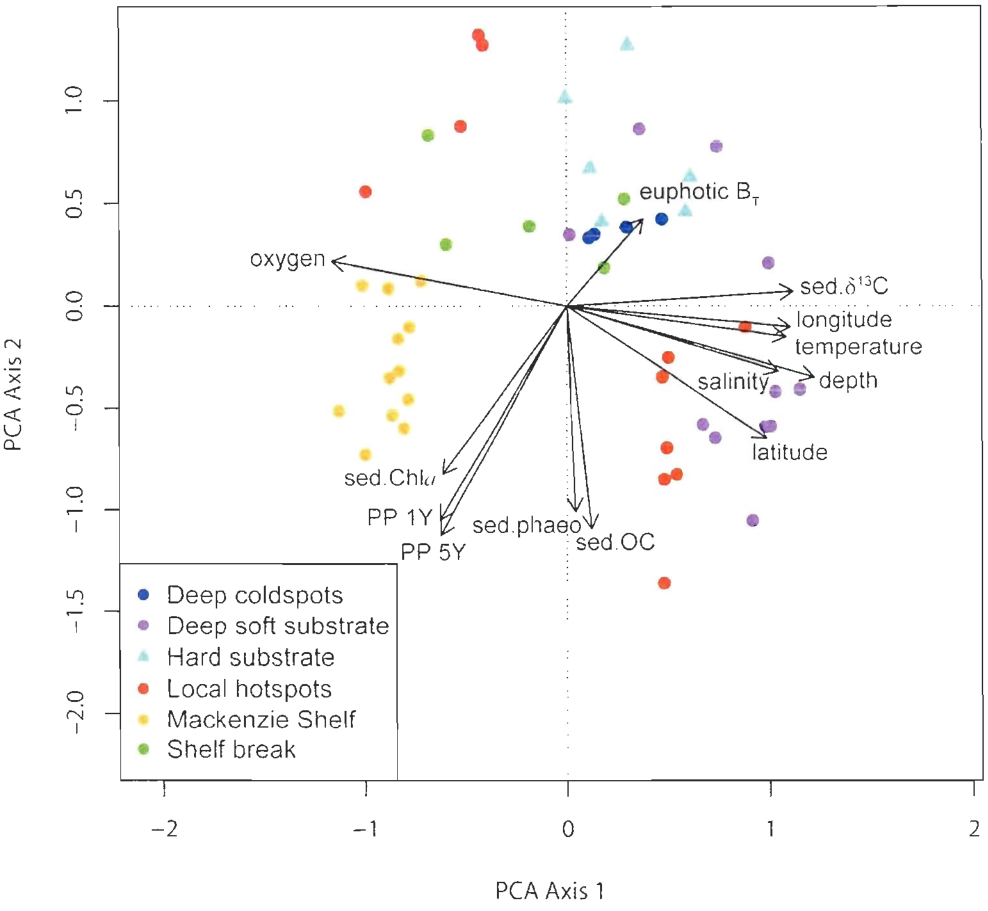
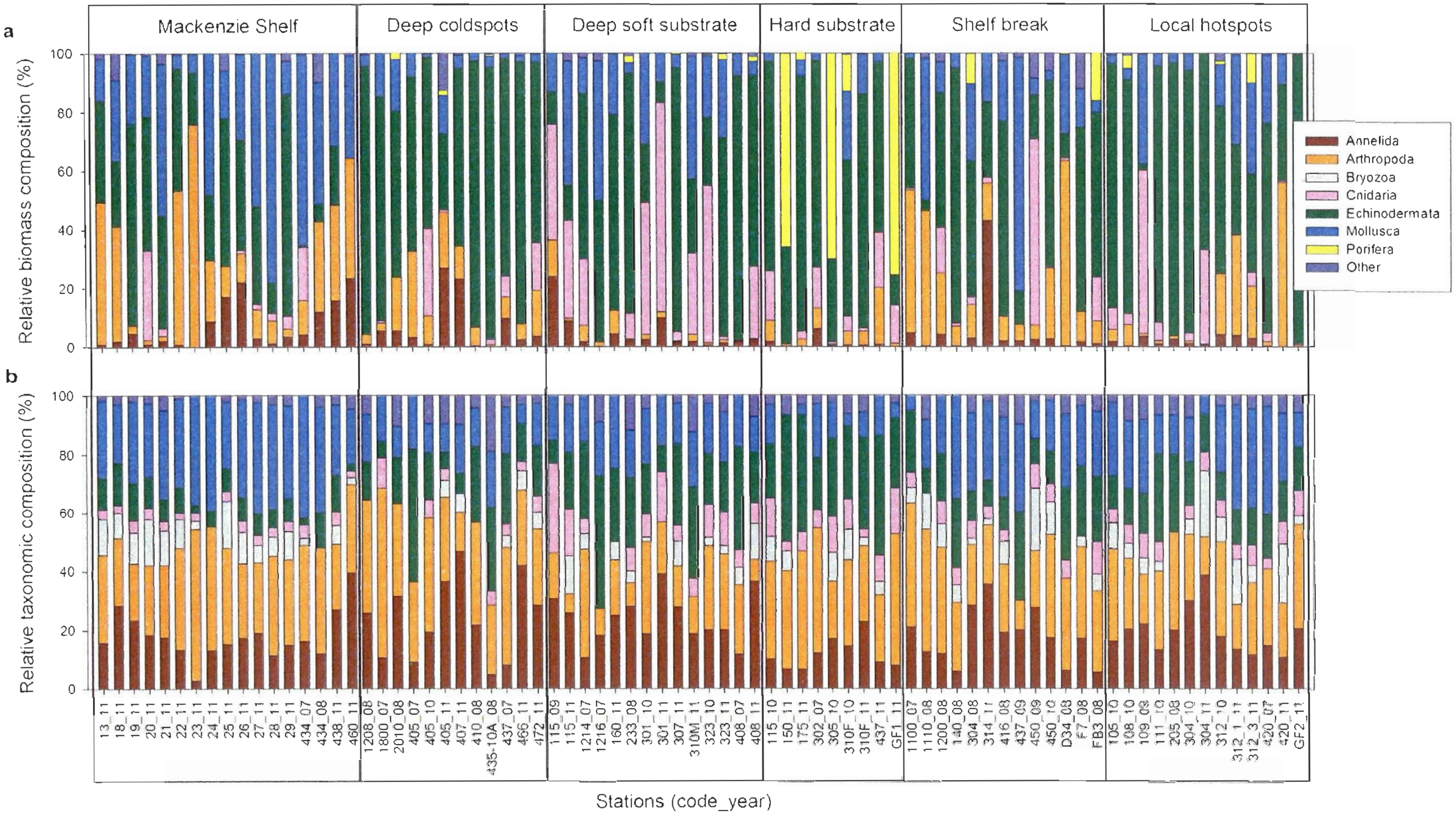
Appendix 2.



Principal Component Analysis (PCA) plot showing the multivariate variation among 50 stations in terms of environmental variables. Vectors indicate the direction and strength of each environmental variable to the overall distribution. Colored symbols correspond to the six megabenthic community clusters defined in this study. The first two principal axes explained 64 % of the variance (λ_1=5.1 and λ_2=3.2).



Station-based variation in mean relative (%) (**a**) biomass composition, and (**b**) taxonomic richness composition for the main phyla sampled across all community clusters. Stations are grouped by community clusters and are organised within clusters by numeric order.Station codes correspond to ArcticNet expedition labels.

CHAPITRE 3

MODÈLES DE PRÉDICTION DE LA DISTRIBUTION DES COMMUNAUTÉS DE LA MACROFAUNE BENTHIQUE DE L'EST DE LA MER DE BEAUFORT ET DU GOLFE D'AMUNDSEN

RÉSUMÉ

Les patrons de variation de la richesse, densité et des communautés de la macrofaune benthique ont été modélisés en fonction de la profondeur, de variables océanographiques et de caractéristiques du sédiment dans le sud-est de la mer de Beaufort et le golfe d'Amundsen. Cette région détient l'effort d'échantillonnage le plus élevé dans l'Arctique canadien et nous avons assemblé toutes les bases de données taxonomiques et environnementales disponibles qui ont été recueillies par le biais de différents programmes scientifiques entre 1973 et 2012 (235 stations). Les communautés de la macrofaune ne variaient pas significativement entre les programmes d'échantillonnage et entre les saisons, ce qui a permis l'évaluation du contrôle environnemental sur la variation spatiale de la distribution des communautés. Les modèles de régressions linéaires multiples et d'arbres de régression multivariable ont révélé que la profondeur et la salinité étaient les principaux facteurs prédictifs de la distribution des communautés à l'échelle régionale, alors que la taille des grains du sédiment était un bon prédicteur de la distribution des communautés à une échelle sous-régionale, sur le plateau continental (< 200 m). Les pigments (phaeopigments et Chl *a*) et la teneur en carbone organique des sédiments de surface n'étaient pas de bons prédicteurs, probablement en raison d'une disparité entre leur variabilité spatio-temporelle par rapport à la variabilité du macrobenthos sur la période de temps considérée. Les modèles prédictifs que nous présentons accroissent notre compréhension de la variabilité spatio-temporelle des communautés de la macrofaune dans

l'Arctique et fournissent une représentation référentielle de leur distribution spatiale afin d'évaluer les impacts naturels et anthropiques à venir dans cette région.

Ce troisième article, intitulé « *Predictive models of macrobenthos patterns in the southeastern Beaufort Sea and Amundsen Gulf* » fut corédigé par moi-même, les professeurs Philippe Archambault, Kathleen Conlan et Alec Aitken, ainsi que mon collègue Ed Hendrycks. L'article a été soumis le 19 juillet 2014 à la revue *Journal of Marine Systems*. En tant que première auteur, ma contribution à ce travail fut l'essentiel de la recherche bibliographique, l'assemblage et l'homogénéisation des bases de données, le traitement statistique des résultats et la rédaction de l'article. Le professeur P. Archambault a fourni l'idée originale, a contribué à l'approche statistique des données ainsi qu'à la révision de l'article. Les professeurs K. Conlan et A. Aitken, ainsi que mon collègue E. Hendrycks, ont fourni une des bases de données du projet et ont contribué à la révision de l'article. Une version abrégée de cet article a été présentée à la *Conférence de l'Année polaire internationale 2012 – De la connaissance à l'action* à Montréal (Canada) au printemps 2012 et a servi en partie à une *Consultation scientifique nationale du secrétariat canadien de consultation scientifique de Pêches et Océans Canada* en novembre 2012 à Winnipeg (Canada).

PREDICTIVE MODELS OF MACROBENTHOS PATTERNS IN THE SOUTHEASTERN BEAUFORT SEA AND AMUNDSEN GULF

ABSTRACT

Variation in macrobenthos richness, density and community composition were modelled in relation to depth, bottom water variables and sediment characteristics in the southeastern Beaufort Sea and Amundsen Gulf. These regions hold the highest sampling efforts across the Canadian Arctic and we synthesized all available faunal and environmental data sets that were collected through different sampling programs over 1973-2012 (235 stations). Macrobenthos communities did not vary significantly between the collecting programs or between seasons, allowing for the evaluation of environmental forcing on spatial variation. Multiple linear regression and multivariate regression tree models revealed that depth and salinity were the main environmental predictors of macrobenthos patterns at the regional scale, while sediment grain size was a good environmental predictor at a sub-regional scale on the shelf (< 200 m). Surface sediment pigments (phaeopigments and Chl a) and organic carbon content were not good predictors, likely due to a mismatch between their spatio-temporal variability relative to the macrobenthos variability over the time period considered. The predictive models that we present increase our understanding of the spatio-temporal variability of macrobenthos communities in the Arctic and provide a reference baseline of the spatial distribution of macrobenthos patterns for evaluating future natural and anthropogenic induced impacts in this region.

***Keywords*:** macrobenthos, community ecology, Arctic, depth, bottom water, sediment grain size, spatio-temporal variability, multivariate regression tree.

INTRODUCTION

Understanding and predicting biodiversity patterns in benthic ecosystems are both necessary and challenging in polar systems facing climate-induced changes, such as the rapid decrease of summertime sea-ice cover in the Arctic (ACIA 2004). Extensive baseline data documenting present marine benthic ecosystem conditions are lacking in many Arctic regions (Archambault *et al.* 2010; Kenchington *et al.* 2011; Wassmann *et al.* 2011), thus preventing our abilities to build reliable predictive models. An exception within the Canadian Arctic is the Canadian Beaufort Sea region where hydrocarbon exploration has spurred field programs since the 1970's (Wacasey 1975; Wacasey *et al.* 1977; Atkinson & Wacasey 1989). With improved logistic capabilities, widespread field programs were revived in the last decade in this region, such as the Canadian Arctic Shelf Exchange Study (CASES) and the Northern Coastal Marine Studies (CCGS *Nahidik* program). Studies based on these data (Aitken *et al.* 2008; Conlan *et al.* 2008; Conlan *et al.* 2013) have greatly improved our understanding of the spatial distribution of macrofaunal communities and of density and biomass patterns in this region. With the accumulation of data from the International Polar Year-Circumpolar Flaw Lead System Study (IPY-CFL) from 2007 to 2008, through research collaborations among the CCGS *Amundsen* program, ArcticNet, BP Exploration Operating Company Limited, ExxonMobil and Imperial Oil from 2009 to 2011, and from the Beaufort Regional Environmental Assessment (BREA) in 2012, there is now a great amount of faunal and environmental data that are available to build compelling predictive models for this region. The purpose of this study is therefore to synthesize all available offshore data sets (> 30 m depth) over 1973-2012 on macrobenthos taxa richness and density in the southeastern Beaufort Sea and Amundsen Gulf regions and produce regional-scale predictive models for richness, density (univariate biodiversity metrics) and communities (multivariate community composition) based on environmental variables sampled at the time of faunal collection. Given that Conlan *et al.* (2008) showed that depth and bottom water physical properties (e.g., temperature, oxygen) had the highest correlation with macrofaunal community distribution in this region, we assume that these relationships will also be detectable with the present larger data set. We therefore hypothesise that these environmental factors will be strong predictors of community structure, while sediment grain size and other sediment characteristics (e.g., sediment organic carbon) are expected to have a weaker relationship.

A key hypothesis adopted in this paper is that the temporal variability across the different sampling programs was negligible considering the well-established long-term integrative responses of macrofaunal communities to their environment, because of the longevity and restrained mobility of many benthic organisms (Pearson & Barnett 1987; Clarke & Warwick 2001). Offshore benthic communities of Arctic regions have inhabited relatively stable environments over the previous decades (Piepenburg 2005). Environmental changes and their related impacts on the biota are expected, however, to increase in rapidity and in intensity in upcoming decades due to climate changes (ACIA 2004) and this assumption of relative stability might not be valid in the future. The export of terrigenous carbon to the Arctic Ocean is expected to increase owing to the predicted increase in precipitation, river runoff and coastal erosion (Carmack & McLaughlin 2001; Piepenburg 2005; Walsh 2008). Furthermore, the predicted reduction in summertime ice cover will certainly lead to increases in storminess, oceanic mixing, ocean wave generation, and coastal flooding (Walsh 2008). Upwelling zones will also be subject to climate change (Carmack & McLaughlin 2001), expanding if ice edges and steep topography are spatially coincident or contracting if the ice edge retreats too far. These changes could result in expansion of an inshore stress-tolerant benthic community over the shelf and contraction of rich communities currently present in upwelling areas (e.g., off Cape Bathurst) (Conlan *et al.* 2008). Biological changes associated with climate change, such as changes in sea-ice algal standing stock, phytoplankton seasonality, zooplankton interception of sinking particulate organic matter (Bluhm & Gradinger 2008) and different bottom predators associated with open water (e.g., gray whales; Conlan *et al.* 2013) will also affect benthic community patterns. We stress, therefore, the importance of the regional predictive models that we present here as a reference for evaluating future temporal and spatial variations in macrobenthic diversity, as well as a strong knowledge base for informed decisions, for example on future oil and gas activities and for the designation of Ecologically and Biologically Significant Areas (EBSAs) (Cobb *et al.* 2014).

MATERIALS AND METHODS

Study area

The Canadian Beaufort Shelf is a relatively broad shelf extending over 64 000 km^2 to the shelf edge at 200 m (O'Brien et al., 2006). The Mackenzie Shelf is bordered by the Mackenzie Trough to the west, the Amundsen Gulf to the east, the Mackenzie River Delta to the south and the Beaufort Sea to the north (Figure 21). The Beaufort Sea and Amundsen Gulf regions are strongly influenced by the Mackenzie River that drains a watershed of 1.7 x 10^6 km^2 and discharges approximately 340 km^3 y^{-1} of freshwater (McLaughlin *et al.* 2004) and 127 million Mt y^{-1} of sediment load (Macdonald *et al.* 2004). The immense quantities of fresh water delivered by the Mackenzie River make the Mackenzie Shelf the most estuarine of all pan-Arctic shelves (Carmack *et al.* 2004). Surface sediments in the study area consist essentially of fine grained material composed of more than 70 % silt and clay (Conlan *et al.* 2008; Conlan *et al.* 2013; Jerosch 2013) discharged by the Mackenzie River or released by coastal erosion (Forest *et al.* 2007). Sand and gravel are largely confined to < 10 m depth and to shelf areas west and east of the Mackenzie Delta (Conlan *et al.* 2008; Jerosch 2013). Surface sediment organic carbon is in large part derived from terrestrial organic matter in areas influenced by either the Mackenzie River plume or by coastal erosion, and is mainly composed of refractory marine material in offshore areas (Morata *et al.* 2008; Magen *et al.* 2010).

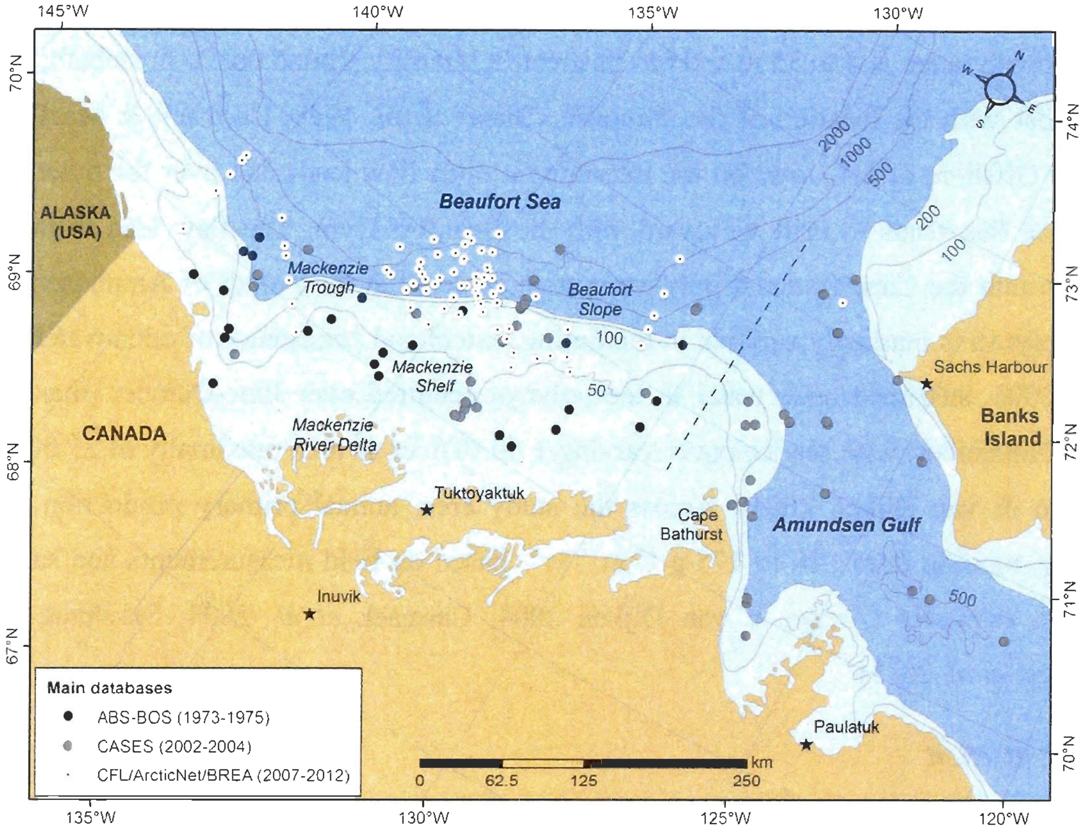


Figure 21. Locations of the 235 stations where macrofaunal samples were collected over 1973-2012 by the three main sampling programs (> 30 m water depth). Dashed line shows the division used in this study between southeastern Beaufort Sea and Amundsen Gulf regions. The shelf break and the transition between the Pacific and Atlantic water masses are both around 200 m, indicated by the two shades of blue.

The water mass vertical structure is composed of the Polar-Mixed Layer (PML; 0-50 m), the Pacific Halocline (PH; 50-200 m) and Atlantic waters (> 200 m) (Carmack & MacDonald 2002). The PML is seasonally influenced by the Mackenzie River discharge and sea-ice melt (Carmack & MacDonald 2002). Ice cover is markedly variable inter-annually, but freeze-up begins generally in early to mid-October, break-up begins in late May and the shelf can be clear of ice by mid-July depending on winds (Carmack & MacDonald 2002). Winter landfast ice extends to about the 20 m isobath, bordered by a *stamukhi* zone of grounded ice and pressure ridges. Active scouring occurs predominantly in the depth range of 8 to 35 m and has its greatest intensity around the 20 m isobath, which coincides with the location of the *stamukhi* (Blasco *et al.* 1998; Carmack & MacDonald 2002). Offshore of the *stamukhi* are intermittent open flaw leads and over the outer shelf, pack ice that tends to drift westward with the Beaufort Gyre. The flaw lead to the east widens into the Cape Bathurst polynya system centered at the mouth of Amundsen Gulf. The polynya is markedly variable in the timing, extent and persistence of open water. Over 1998-2002, sustained open water in the polynya occurred over June-October (maximally April-November) with sea ice cover varying ± 40 % over an area maximally of 25 000 km^2 (Arrigo & van Dijken 2004). Across the study area, annual primary production varies greatly, ranging from ~10 to 175 $g\ C\ m^{-2}\ yr^{-1}$ based on field measurements and satellite-derived estimates (Arrigo & van Dijken 2004; Carmack *et al.* 2004; Sakshaug 2004; Bélanger *et al.* 2013).

Data collection

This study is based on sampling conducted partially within the framework of the (1) Arctic Biological Station program-Biological Oceanography Section (ABS-BOS) from 1973 to 1975 (Wacasey *et al.* 1977), (2) CCGS *Sir Wilfrid Laurier* program and CASES from 2002 to 2004 (collectively called the CASES program) (Aitken *et al.* 2008; Conlan *et al.* 2008; Conlan *et al.* 2013), (3) IPY-CFL from 2007 to 2008 (Fortier *et al.* 2012), (4) through research collaborations among the CCGS *Amundsen* program, ArcticNet, BP Exploration Operating Company Limited, ExxonMobil and Imperial Oil (collectively called the ArcticNet program) from 2009 to 2011, and (5) BREA in 2012 (BREA 2012).

Faunal data collection

Macrobenthos communities were sampled at 235 stations from 1973 to 2012 between April and November through different scientific programs and onboard different research vessels (Figure 21, Table 9). Station depths ranged from 31 to 1072 m, mostly below the most intense ice scouring zone of 8-35 m (Blasco *et al.* 1998; Carmack & MacDonald

2002). Faunal samples were collected mostly with a USNEL box corer (0.25 m^2), except from 1973 to 2002 where different grab models were used (Table 9). Due to shared sediment requirements, on average 0.12 ± 0.05 m^2 of sediment were sieved from each box core or grab sample. All box core and grab catches were washed under running seawater onboard over a 0.4 mm sieve during the CASES program and over a 0.5 mm sieve during all other programs. CASES samples were rewashed in the lab on 0.5 mm mesh (erroneously reported as 0.4 mm mesh in Conlan *et al.* 2008), resulting in all macrobenthic invertebrates considered here being $\geq$ 0.5 mm size.

Taxa were preserved in a 4 to 5 % seawater-formaldehyde solution buffered with sodium tetraethylborate for later identification in the lab and then transferred in 70 % ethanol for long-term storage. Only specimens with the head-part intact were counted and identified to the lowest possible taxonomic level. Taxonomic identifications were conducted by specialists at the Canadian Museum of Nature (CMN) and University of Saskatchewan (U. Sask., SK, Canada) for CASES samples and at the Benthic Ecology Lab (*Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, QC, Canada* (UQAR-ISMER)) for samples collected after 2004. Samples gathered through the CASES program are housed at the CMN, while samples gathered through CFL, ArcticNet and BREA programs are housed at UQAR-ISMER. Details on the taxonomic identification of the ABS-BOS data set are available in Wacasey *et al.* (1977).

Table 9. Description of field programs (years, ship cruises, samplers and labs where invertebrate identifications were conducted), and number of stations sampled by the different programs and included in the four different data analysis scenarios according to environmental variables that were available.

Scientific program	Years sampled	Ship cruise	Sampler	Lab identifying the fauna	No. of stations	No. of stations for data subset #1	No. of stations for data subset #2	No. of stations for data subset #3	No. of stations for data subset #4
ABS-BOS	1973 to 1975	*North Star of Herschel Island*[a], M.V. *Theta*[b] & *Pandora II*[c]	Wildco Ponar grab[a], Petterson grab[b], Wildco Petersen grab[c]	ABS-BOS	25	25	25	0	0
CASES	2002 to 2004	CCGS *Sir Wilfrid Laurier*[d], *Radisson*[d] & *Amundsen*	van Veen grab[d] & box corer	CMN, U. Sask.	125	125	116	94	40
CFL	2007 to 2008	CCGS *Amundsen*	box corer	UQAR-ISMER	4	4	2	0	0
ArcticNet	2009 to 2011	CCGS *Amundsen*	box corer	UQAR-ISMER	58	56	49	32	32
BREA	2012	F/V *Frosti*	box corer	UQAR-ISMER	23	23	23	23	23
TOTAL					235	233 (99 %)	215 (91 %)	149 (63 %)	95 (40 %)

ABS-BOS: Arctic Biological Station-Biological Oceanography Section; CMN: Canadian Museum of Nature; U. Sask.: University of Saskatchewan; UQAR-ISMER: *Université du Québec à Rimouski-Institut des sciences de la mer de Rimouski.* [a]1973; [b]1974; [c]1975; [d]2002.

Data subset #1: depth (m), temperature (°C), salinity
Data subset #2: subset #1 + sediment grain size (% sand = 100 - % silt + clay)
Data subset #3: subset #2 + sediment organic carbon content (%) and sediment $\delta^{13}C$ (‰)
Data subset #4: subset #3 + sediment pigment (phaeopigments and Chl *a*; mg m^{-2})

Bottom water variables

Bottom water physical properties that were available at almost all stations at the time of faunal collection were included in the present analysis (n = 233 stations). Near-bottom water temperature (°C) and salinity were determined at 0.5 to 10 m above the seafloor. Water mass partition based on temperature and salinity data was done by cluster analysis on Euclidean distance (results not shown). Few stations were located in the PML (0-50 m) and their salinity and temperature were not distinct enough to be considered separately from the PH (50-200 m), thus stations clustered in two major water masses, that we call hereafter Pacific and Atlantic water mass. Based on our data, the Pacific water mass (n = 137 stations) was characterized by salinities ranging from 29.15 to 33.84 and temperatures ranging from -1.78°C to -0.10°C, while the Atlantic water mass (n = 98 stations) was characterized by salinities ranging from 34.16 to 34.86 and temperatures ranging from -0.59°C to 0.55°C. The transition from the Pacific to the Atlantic layer was observed between 200 and 225 m in agreement with the water mass distribution observed in other studies carried out in the region (Carmack & MacDonald 2002; McLaughlin *et al.* 2005; Forest *et al.* 2007). Dissolved oxygen concentration was not available at all stations (mostly for the 1973-1975 ABS-BOS data set) and was therefore not included here. Generally bottom water dissolved oxygen concentrations were high over the region and ranged from 5.1 to 9.1 ml l^{-1} between 2002 and 2012.

Surface sediment variables

We evaluated if the spatial distribution of different surface sediment variables was related to macrofaunal patterns. The variables considered were: sediment Chl *a* content, sediment phaeopigments (degraded chlorophyll), sediment organic carbon, sediment $\delta^{13}C$ and sediment grain size. No sediment pigment data were available in 2002 and from 2007 to 2009. Sediment pigment data in 2003 and 2004 during the CASES program are reported in Bessiere *et al.* (2007). From 2010 to 2012, pigment concentrations were analysed fluorometrically at UQAR-ISMER following a modified protocol by Riaux-Gobin and Klein (1993). Sediment pigment data are expressed in mg m^{-2} and were available at 95 stations. CASES sediment organic carbon content and stable organic carbon isotopic composition ($\delta^{13}C$) data were analysed at the University of Calgary (AB, Canada) and are available through the published studies of Conlan *et al.* (2008) and Conlan *et al.* (2013). Additional sediment $\delta^{13}C$ data in 2003 and 2004 are presented in Morata *et al.* (2008). From 2010 to 2011, sediment organic carbon content and sediment $\delta^{13}C$ were determined after acidification (HCl 10 %) using an ECS 4010 elemental analyzer coupled with a Delta^{Plus} XP isotope ratio mass spectrometer (IRMS) at the Marine Chemistry and Mass Spectrometry Laboratory (UQAR-ISMER), while in 2012 they were determined using a Carlo-Erba EA 1108 Elemental Analyzer coupled with a Finnigan Delta^{Plus} IRMS at the University of Waterloo Environmental Isotope Laboratory. Sediment organic carbon content is expressed as % of total sediment dry weight and was available at 149 stations. Sediment $\delta^{13}C$ data are reported in standard delta notation in ‰ with respect to Vienna Pee Dee Belemnite (VPDB) and are available at 154 stations. Sediment $\delta^{13}C$ is used here as a measure of the contribution of terrestrial organic carbon input in order to investigate the influence of coastal erosion and Mackenzie River sediment discharge on benthic community structure. Lighter sediment isotopic $\delta^{13}C$ values (-28 to -26‰) are typical of terrigenous organic matter while heavier isotopic $\delta^{13}C$ values (-24 to -20‰) are typical of marine production (Stein & Macdonald 2004). Sediment grain size data are presented here as two quantitative categories: sum of silt and clay (%; < 63 μm), and sand (%; 63 μm – 2 mm). We only used % sand in subsequent data analysis because one grain size category is the reverse of the other and thus both categories cannot be retained at the same time in predictive models. CASES sediment grain size data were analysed at the University of Calgary and are available through published studies of Conlan *et al.* (2008) and Conlan *et al.* (2013). From 2010 to 2012, sediment grain size samples were analysed at UQAR-ISMER with a Beckman Coulter™ LS 13 320. Some missing grain size data (n = 27 stations) were estimated based on the geostatistical mapping of surficial sediment types of the Beaufort Shelf in Jerosch (2013). Remaining missing grain size data could not be estimated, resulting in a total of 215 stations where sediment grain size data were available.

Data analysis

Homogenisation of faunal data sets

Prior to analyses, large sized meiofauna that were present in the data sets were eliminated (i.e., nematodes, ostracods and foraminifera), as meiofaunal groups are mostly not retained on 0.5-mm sieves (Eleftheriou & McIntyre 2005; Giere 2009). Ostracods have been included in some previous Arctic studies on macrobenthos (e.g., Denisenko *et al.* 2003; Conlan *et al.* 2008; Cochrane *et al.* 2009; Blanchard *et al.* 2013b; Conlan *et al.* 2013) due to large size of some taxa (e.g., *Philomedes* sp. and *Scleroconcha* sp.), but we had to exclude them here because they were not counted in all years. Few colonial organisms were present in the faunal data sets (i.e., Bryozoa, Hydrozoa and Nephtheidae (soft corals)) and, when present at a station, their abundance was assumed at 1 individual. To remove potential bias caused by identifications performed in different labs over different sampling programs and years, we scaled all taxa that were identified at the species level to the genus level. We also had to merge some taxa at a higher level of taxonomic resolution (i.e, family, order, class or phylum), because the knowledge of the taxonomy of all faunal groups was variable among the labs (e.g., Anthozoa, Bryozoa, Capitellidae, Holothuroidea, Hydrozoa, Priapulida, Sipuncula, etc.). Finally, taxonomic names of all faunal data sets were verified at the same time using the World Register of Marine Species (WoRMS, (Appeltans *et al.* 2014).

Statistical analyses

Macrobenthic richness and abundance may vary over time due to environmentally-driven changes (e.g., Kortsch *et al.* 2012) and we therefore evaluated first if richness and density were displaying significant differences among the three main databases that comprised different sampling periods (Table 9). For a sound comparison we only compared the stations within the Beaufort Sea region that shared a similar depth range across the three main databases (i.e., from 31 to 441 m) by using an analysis of variance (one-way ANOVA with the factor sampling program). To meet assumptions of normality and homogeneity of variances, square-root transformation was applied to richness and fourth-root transformation to density.

Multiple linear regression models were used to model richness and density with environmental factors. We performed four models for each response variable (for a total of eight models) considering four subsets of environmental factors because the latter were not available at each station (Table 9). The best subset solution method using Akaike's information criterion (AIC) was applied to select significant environmental predictors among all available environmental variables. All final best subset regression models were validated for the following assumptions: normality of residuals was examined by plotting theoretical quantiles vs. standardized residuals (Q-Q plots) and homogeneity of variance was assessed by plotting standardized residuals vs. fitted (predicted) values. Because distributions of residuals were skewed in all models, the same transformations as above were applied to richness (square-root) and density (fourth-root). Natural logarithm transformation or square-root transformation were also applied to certain environmental variables until the assumptions were met by each of the final models. Possible outliers with severe influence on the final models were identified using Cook's Distance (D), but none had $D > 1$ (Quinn & Keough 2002). We tested for collinearity of predictors in the four subset models using the variance inflation factor (VIF), with $VIF > 10$ indicating critical collinearity (Quinn & Keough 2002), but they all had $VIF < 10$.

For multivariate analysis, we discarded taxa only found at one station (84 taxa), for a total of 294 unique taxa found minimally at two stations. Singletons in multivariate analysis are prone to random and uninterpretable fluctuations, and it is recommended to remove them to allow for better detection of the underlying community similarities (Clarke & Warwick 2001). To confirm that the temporal variability in community composition over 1973-2012 was small or insignificant, we used an analysis of similarity (one-way ANOSIM), a non-parametric procedure based on rank similarities (Clarke & Warwick 2001). Community composition was compared among the three main sampling programs (range depth of 31-441 m; same procedure as for the above ANOVA) and among sampling seasons (summer: June to August vs. fall: September to November; two stations sampled in April 2004 were not considered in this analysis). ANOSIM was also used to compare community composition among water masses (Pacific vs. Atlantic) and regions (Beaufort Sea vs. Amundsen Gulf). All ANOSIM tests were performed using Bray-Curtis similarity on square-root transformed density data.

Multivariate regression trees (MRT) (De'Ath 2002) were used to partition the stations based on the relationships between community composition with environmental variables (based on Hellinger-standardized density data; Legendre and Gallagher 2001). The same four data subsets used for multiple regression models were again considered in these MRT analyses. The MRT procedure results in a constrained or supervised clustering with the final objective being focused on the best predictive power of a selection of the environmental variables considered. The result of MRT is a 'tree' showing a partition of terminal groups of stations (called 'leaves') and where each successive partition ('split') is defined by a threshold value of a particular environmental variable. In other words, each leaf represents a community defined by the environmental variable values that best define its habitat. The threshold values of the environmental variables make the MRT a useful tool for practical environmental management. There are several advantages to MRT analysis, but the most important is that no assumptions are required regarding data structure, in contrast to many other multivariate techniques (De'Ath 2002). MRT analysis has an inherent property of designating at the first splits the explanatory variables that operate at broader spatial scales and designating in subsequent splits the variables that typically operate at finer spatial scales (Ruppert *et al.* 2010) making it a multivariate analysis tool that can be applied across different scales of investigation. The performance of each tree was assessed by prediction error through cross-validation run 1000 times (called cross-validated relative error (CVRE); CVRE near 0 = perfect predictors; CVRE near 1 = poor set of predictors). To delineate an optimal tree size with a consistent minimum CVRE, the 1 standard error rule (Borcard *et al.* 2011) along with our parsimonious criterion to have no more than 10 communities were used to determine the appropriate number of communities per data subset model. We compared these four predictive subset models of communities with an unconstrained method of cluster analysis to determine whether the MRT community partitions reflected the community composition variance alone. Unconstrained community clusters were determined using Ward's minimum variance clustering (Ward 1963) on Hellinger-standardized density data (Legendre & Gallagher 2001). To find indicator taxa within each community cluster, the indicator value index (IndVal) method of Dufrêne and Legendre (1997) was applied. This index measures the association between a taxon and a cluster of stations and is calculated as the product of the relative frequency and relative average density of taxa within clusters. Statistical significances of indicator taxa were tested by random permutations of stations (9999 permutations). We generated a consensus of the indicator taxa by presenting those of the top five indicator taxa for each cluster analysis (i.e., the unconstrained clustering plus the four constrained clustering) that were common to at least four of the five cluster analyses.

ANOSIM tests were performed using PRIMER-E software version 6 (Clarke & Gorley 2006). All other tests were performed using the statistical package R version 3.0 (R Core Team 2013). Statistical significance at $\alpha < 0.05$ was used for all statistical tests. The distribution of environmental variables and macrofaunal richness and density were mapped with ArcGIS 9.3.1 with color bins defined by the Jenks iterative method which minimizes within class difference and maximizes between class differences (Jenks & Caspall 1971). In the case of close station locations, the dot with the largest value was mapped on top. Distributions of benthic communities were identified and mapped according to the depth zonation.

RESULTS

Spatial patterns and environmental predictors of richness and density

The aggregation of all macrofaunal data sets available over 1973-2012 resulted in a macrofaunal inventory of 378 taxa across 14 phyla. Sampling locations differed in the three periods (Figure 21) with the ABS-BOS samples mostly on the shelf to the west of Cape Bathurst, the CASES samples both on and off the shelf and spanning the Mackenzie Shelf and Amundsen Gulf, and the CFL/ArcticNet/BREA samples on and off the Mackenzie Shelf. Mean richness (number of taxa station^{-1}) of the CASES database was significantly lower ($p = 0.015$) than in the historical 1973-1975 data set (Figure 22b). However, there was no significant difference in mean density (ind. m^{-2}) (Figure 22d). Results on difference in mean richness and mean density among the three main programs remained identical when taking into account two depth zones (shelf and slope) nested within the main factor programs (two-way nested ANOVA; results not shown). Macrofaunal richness varied between 1 and 84 taxa station^{-1} (on average 28 ± 15 taxa station^{-1}) and macrofaunal density varied between 8 and 16 880 ind. m^{-2} (on average 1876 ± 2375 ind. m^{-2}) (Figure 23). Both richness and density were highest near the Mackenzie Trough, on the Mackenzie Shelf and near Cape Bathurst (orange and red colored stations), and were lowest mainly on the Beaufort Slope and in deep areas of the Amundsen Gulf (blue colored stations) (Figure 23). A significant correlation between richness and density confirms the similarity of their spatial patterns (Pearson's r = 0.64, $p < 0.001$).

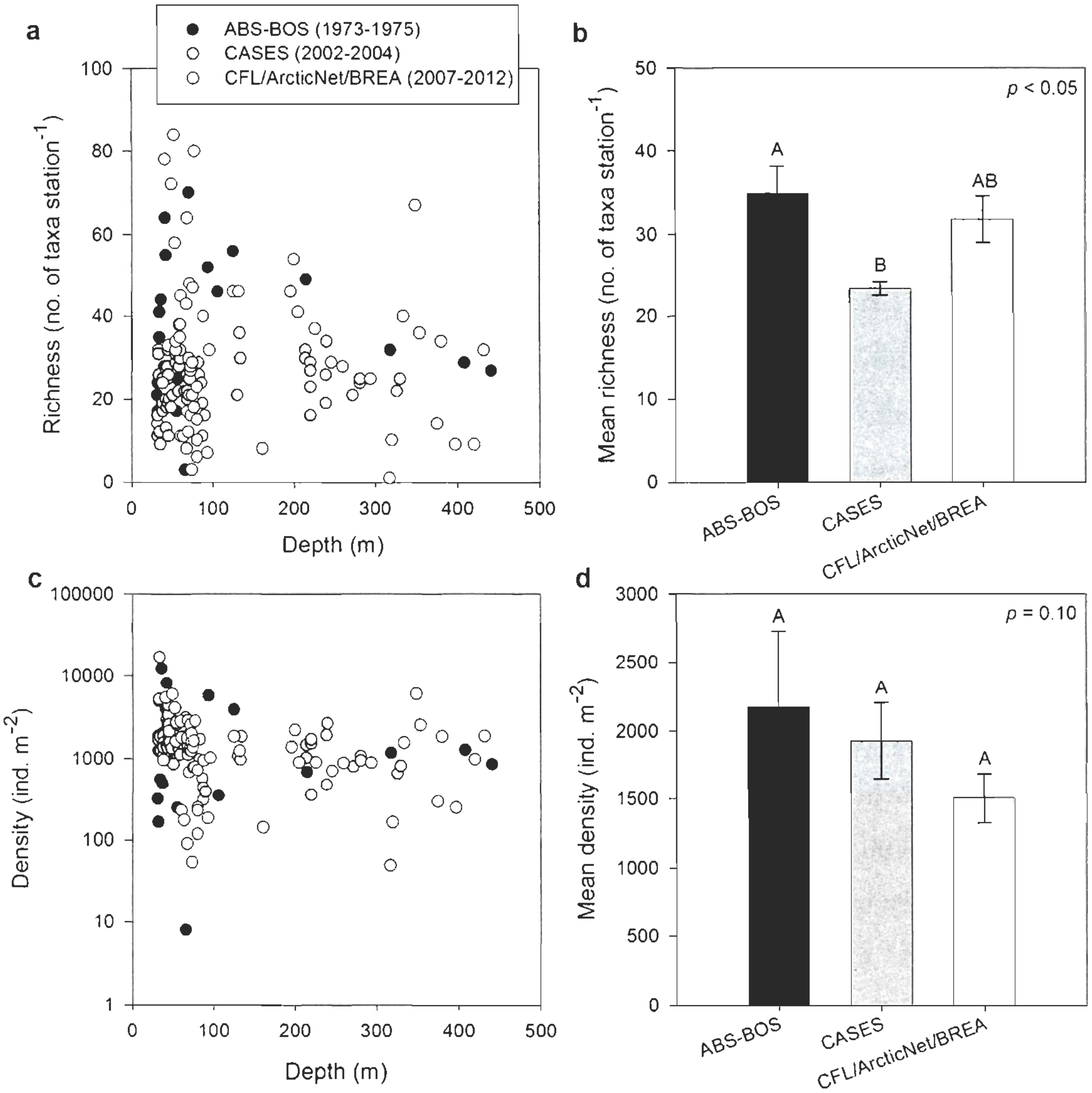


Figure 22. Comparisons of macrofaunal richness (number of taxa station^{-1}) and density (ind. m^{-2}) among the three main sampling programs in the Beaufort Sea region for the depth range 31-441 m. (**a, c**) scatter of data in relation to depth; (**b, d**) mean ± standard error (n in Table 11) for each main sampling program. Letters (A, B) indicate significant differences (one-way ANOVA).

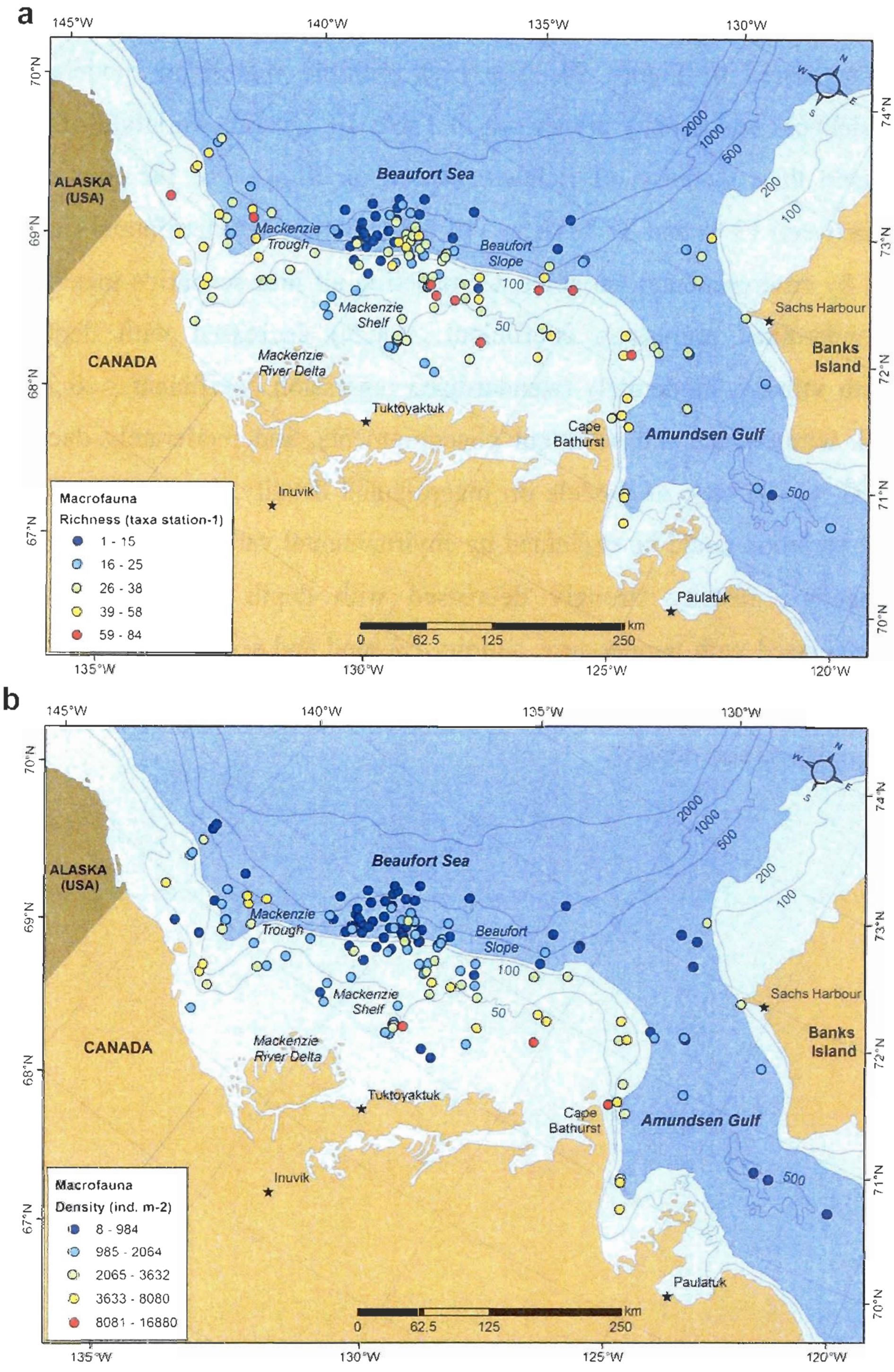


Figure 23. Distribution of macrofaunal (**a**) richness (number of taxa station^{-1}), and (**b**) density (ind. m^{-2}) sampled in the southeastern Beaufort Sea and Amundsen Gulf regions over 1973-2012.

Spatial distributions of environmental variables used for multiple linear regression models are presented in Figure 24. The best multiple regression models explaining variation in richness and density are shown in Table 10. Overall, variation of density was better explained than variation of richness (based on $R^2_{adj.}$). For the four data subsets considered, between 13 % and 37 % ($R^2_{adj.}$) of the variation in macrofaunal richness could be explained by environmental variables. Considering all four scenarios together, richness strongly (standardized regression coefficient > |0.5|) decreased with depth, strongly increased with salinity, moderately (standardized regression coefficient < |0.5|) increased with % sand, temperature and sediment phaeopigments, and moderately decreased with sediment $\delta^{13}C$. In the case of models on macrofaunal density, between 19 % and 58 % ($R^2_{adj.}$) of the variation could be explained by environmental variables. Considering all four scenarios together, density strongly decreased with depth and sediment $\delta^{13}C$, and moderately increased with temperature, salinity, % sand and sediment organic carbon. For the data subset #4, sediment Chl *a* was not retained as an environmental predictor of macrofaunal richness and density.

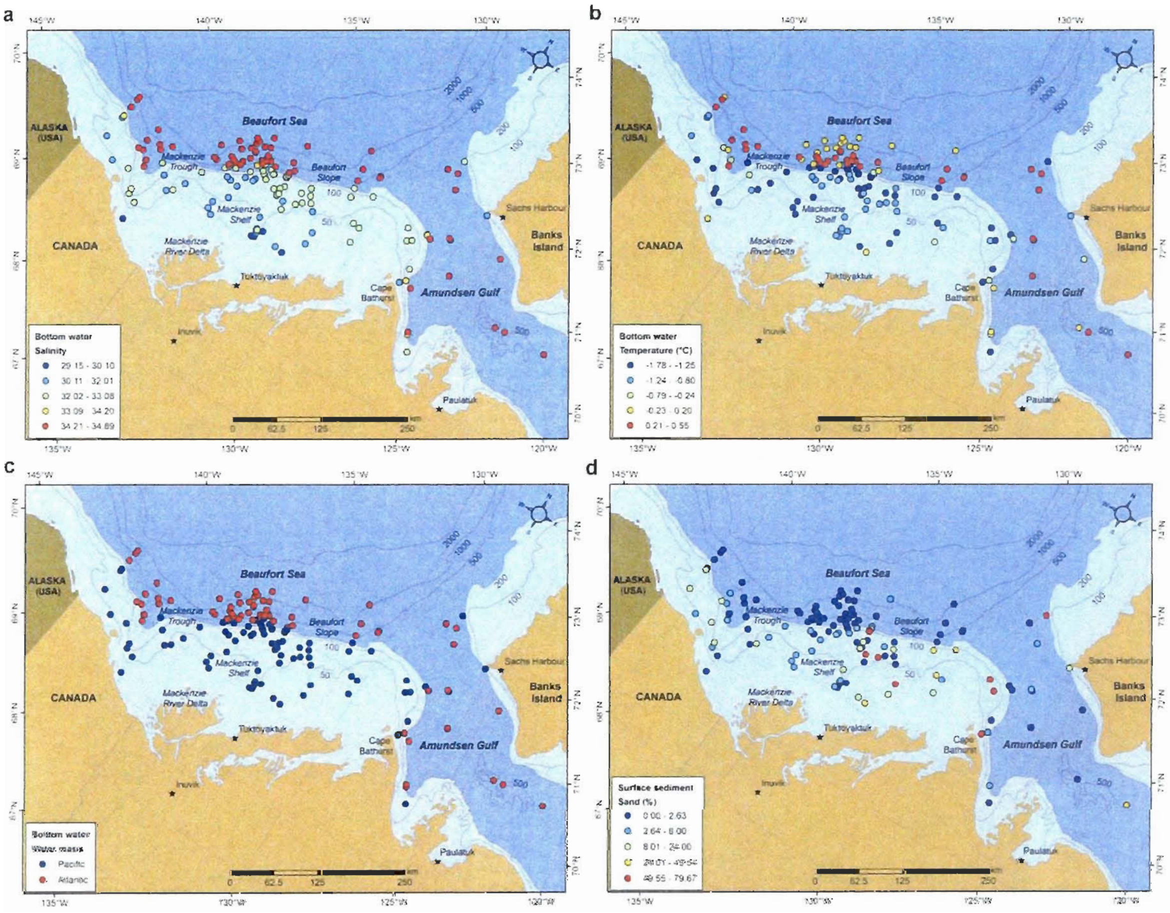


Figure 24. Distribution of bottom water and sediment characteristics measured at the time of macrofaunal sampling in the southeastern Beaufort Sea and Amundsen Gulf over 1973-2012. (**a**) salinity; (**b**) temperature (°C); (**c**) water mass (Pacific *vs.* Atlantic); (**d**) sand (%; 100 - % silt + clay); (**e**) sediment organic carbon (%); (**f**) sediment $\delta^{13}C$ (‰); (**g**) sediment phaeopigments (mg m^{-2}); (**h**) sediment Chl a (mg m^{-2}).

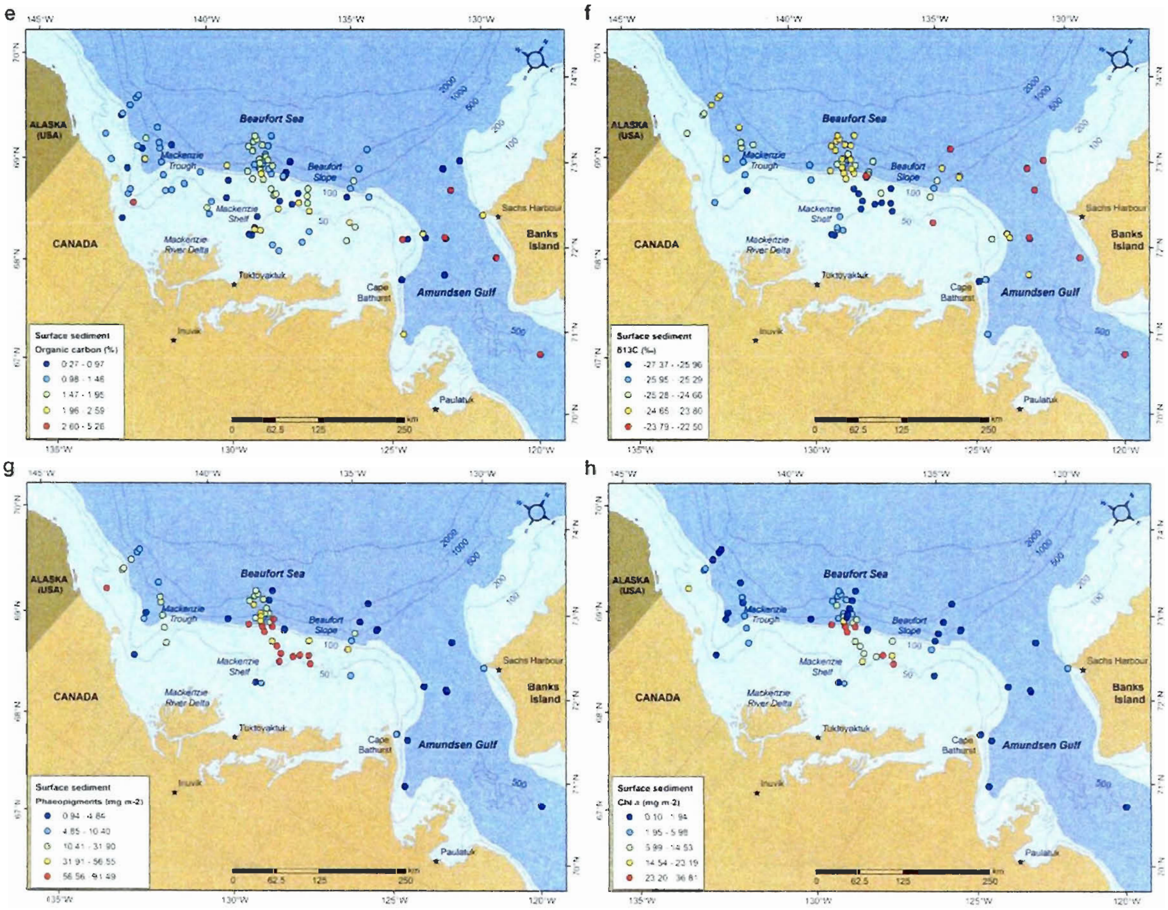


Figure 24 continued. (**e**) sediment organic carbon (%); (**f**) sediment $\delta^{13}C$ (‰); (**g**) sediment phaeopigments (mg m^{-2}); (**h**) sediment Chl a (mg m^{-2}).

Table 10. Multiple linear regression model results for richness (number of taxa station^{-1}; square-root transformation) and density (ind. m^{-2}; fourth-root transformation) against environmental factors. Four models are presented for each response variable considering four data subsets according to available environmental factors. For each best-solution model retained, standardized regression coefficients of environmental predictors, R^2 and adjusted R^2 ($R^2_{adj.}$) are presented. Data subsets as in Table 9.

	Data subset #1		Data subset #2		Data subset #3		Data subset #4	
Variable	Richness	Density	Richness	Density	Richness	Density	Richness	Density
ln(depth)	-0.98***	-1.08***	-0.71***	-0.88***	-0.73**	-0.35**	nr	-0.78***
temperature	nr	0.23*	nr	0.24*	nr	0.34**	0.31**	0.71***
salinity	0.77***	0.52***	0.63***	0.38*	0.87***	nr	nr	nr
[a] or [b] (sand)			0.19**	0.14*	[a]0.20*	[a]0.45***	[b]0.45***	[b]0.25*
[c] or [d] (sediment OC)					nr	[c]0.34***	nr	[d]0.14^{ns}
sediment $\delta^{13}C$					-0.38***	-0.60***	-0.52***	-0.57***
ln(sediment phaeopigments)							0.33**	nr
ln(sediment Chl *a*)							nr	nr
No. of stations	233	233	215	215	149	149	95	95
(% over 235 stations)	(99 %)	(99 %)	(91 %)	(91 %)	(63 %)	(63 %)	(40 %)	(40 %)
No. of predictors retained	2	3	3	4	4	5	4	5
R^2, $R^2_{adj.}$	0.16, 0.15	0.23, 0.22	0.14, 0.13	0.21, 0.19	0.20, 0.18	0.41, 0.39	0.40, 0.37	0.60, 0.58
F	21.11***	23.11***	11.92***	13.68***	8.86***	19.76***	14.74***	27.23***

nr: indicates that the environmental factor was not retained in the model; ns: indicates that the environmental predictor was retained but not significant in the model; ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. Data transformation: [a] fourth-root, [b] ln(data + 1), [c] ln, [d] square-root.

Spatial patterns and environmental predictors of macrobenthic communities

Community composition was not different among the stations sampled in different seasons and by the three main sampling programs (Table 11). ANOSIM R values were very close to 0, thus showing great overlap in community composition between categories (Clarke & Warwick 2001). Community composition differed significantly among water masses (Pacific vs. Atlantic) and among depth categories (shelf vs. slope), but not between the Beaufort Sea and Amundsen Gulf regions (Table 11).

Table 11. ANOSIM results on temporal and spatial variability considering different categorical factors. A global R ≈ 1 indicates categories with completely distinct taxonomic composition and global R ≈ 0 indicates complete overlap in taxonomic composition between categories (see text for details). [1]One way; [2]two-way nested.

Variability type	No. of stations per category	Global R	p (9999 perm.)
Temporal variability			
Season[1]	Summer: 125 Fall: 108	0.045	0.0004
Scientific programs (only for the overlapping depth range of 31-441 m in the Beaufort Sea region)[1]	ABS-BOS: 25 CASES: 62 CFL/ArcticNet/BREA: 56	0.245	0.0001
Scientific programs (as above, but taking into account two nested depth zones: shelf/slope)[2]	ABS-BOS: 21 shelf/4 slope CASES: 48 shelf/14 slope CFL/ArcticNet/BREA: 40 shelf/16 slope	-0.056	0.66
Spatial variability			
Region[1]	Beaufort Sea: 178 Amundsen Gulf: 57	-0.033	0.82
Water mass[1]	Pacific: 137 Atlantic: 98	0.346	0.0001
Depth[1]	Shelf (< 200 m): 131 Slope (≥ 200 m): 104	0.352	0.0001

The unconstrained cluster analysis resulted in six well-defined community clusters (Figure 25a). The clusters were coded by depth, from shallowest (A) to deepest (B) (Figure 25b). Spatial distributions of environmental variables used for the four constrained cluster analyses (MRT) are presented in Figure 24. Based on our optimal and parsimonious tree size criteria (see Data analysis) and on the four data subsets considered, MRT cluster analyses resulted in five main clusters for MRT #1, six clusters for MRT #2 and MRT #3, and seven clusters for MRT #4 (Figure 26). These best-solution models explained between 19 % and 37 % (R^2) of the variation in macrofaunal composition (Table 12). For all four data subset scenarios, bottom water salinity and depth were always either the primary or secondary environmental predictors (Figure 26). Sand was a secondary or tertiary predictor in MRT #2 and MRT #3. Bottom water temperature was a tertiary predictor in the first three MRTs. Sediment Chl *a* was a secondary and sediment organic carbon a quaternary predictor in the last scenario (MRT #4). Spatial distributions of the community clusters are shown below each tree (Figure 26). Following the same logic as above, the community clusters were coded by depth, from shallowest (A) to deepest (F). Taxa that consistently typified at least four of the five cluster analyses are presented in Table 12. All of the top five indicator taxa for each community cluster across the different cluster analyses are provided in Appendix 3.

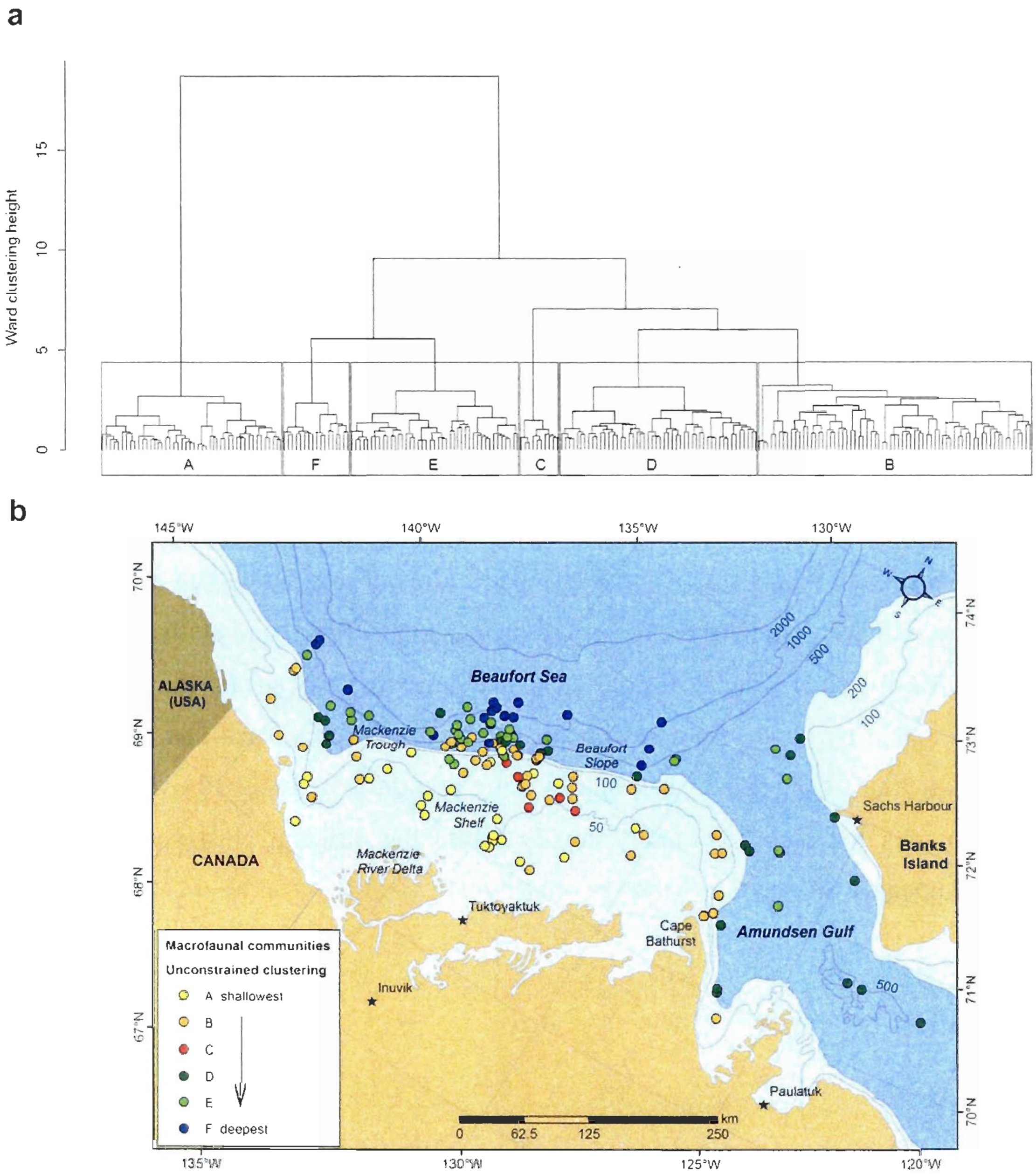


Figure 25. Macrofaunal community clusters defined by unconstrained cluster analysis (Ward's minimum variance) on 235 stations. (**a**) Cluster dendrogram; (**b**) Distribution of clusters from the shallowest (A) to the deepest (F).

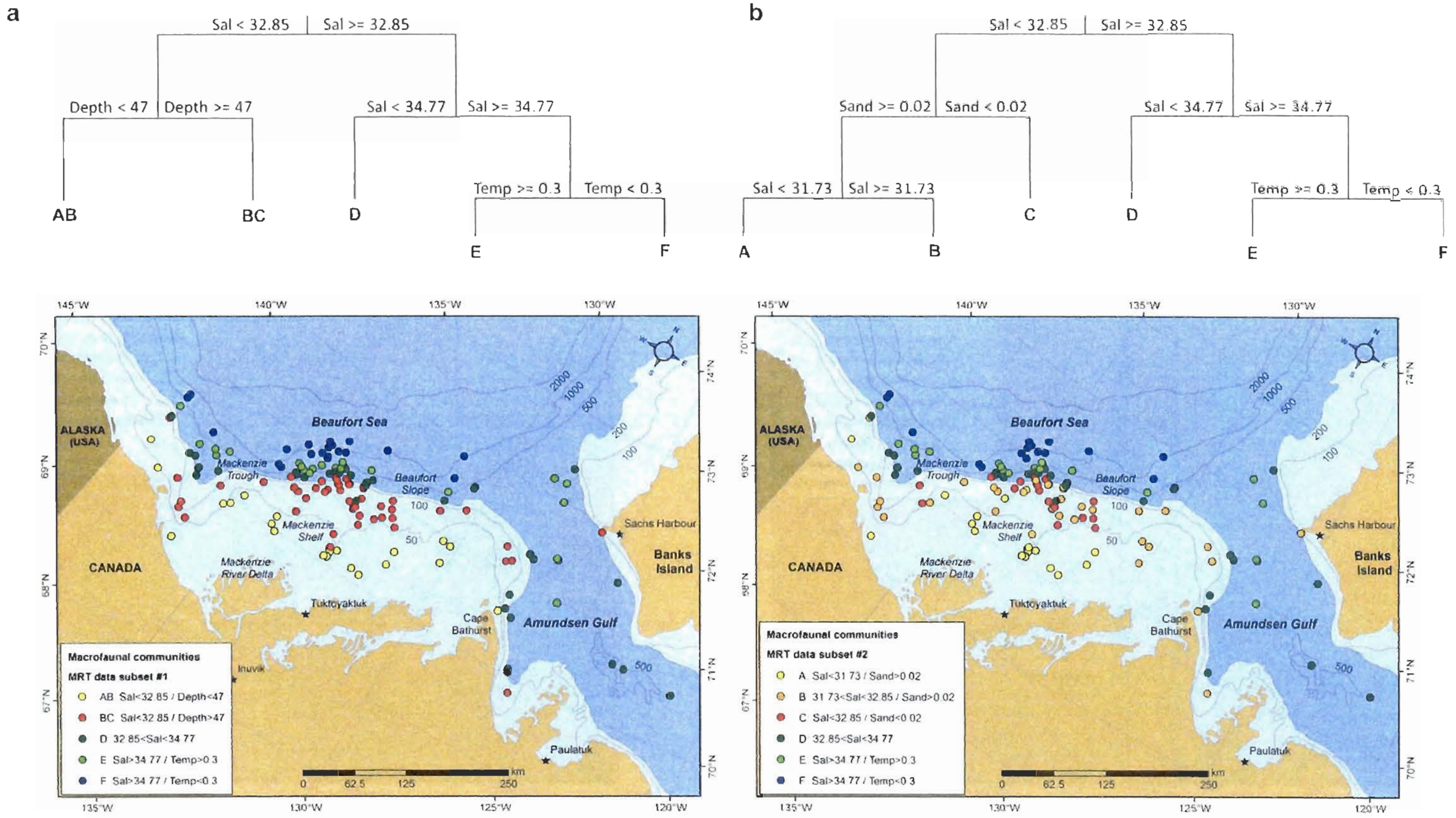


Figure 26. Macrofaunal community clusters defined by constrained cluster analysis of the four data subsets described in Table 9. The MRT tree is shown at the top and the distribution of the clusters is shown on the map below. The clusters are ordered by depth (from A to F). (**a**) Data subset #1 (233 stations); (**b**) Data subset #2 (215 stations); (**c**) Data subset #3 (149 stations); (**d**) Data subset #4 (95 stations).

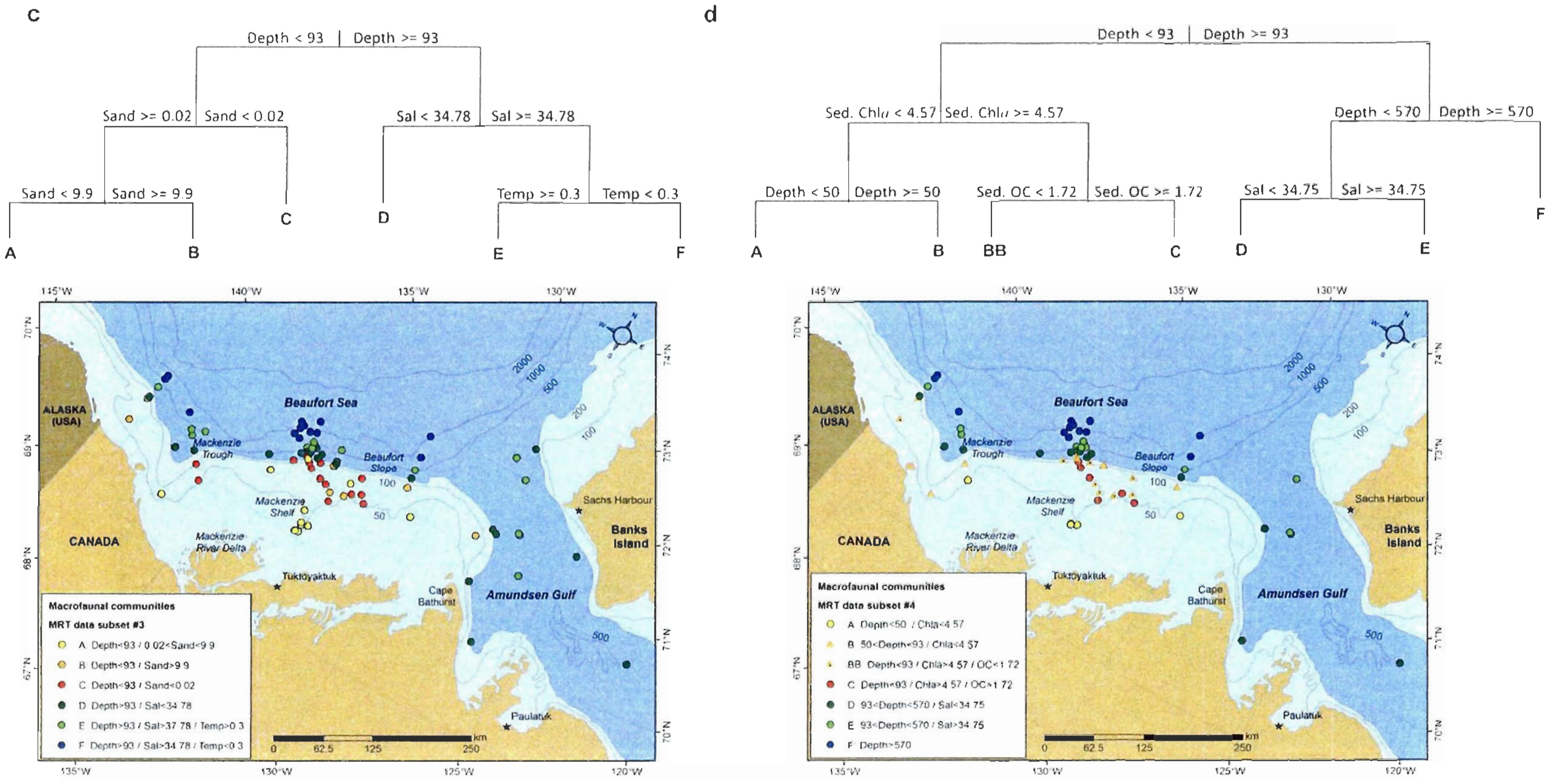


Figure 26 continued. (**c**) Data subset #3 (149 stations); (**d**) Data subset #4 (95 stations).

Table 12. List of significant indicator taxa that were common to at least four clustering over five (including the unconstrained (Ward) and the four constrained (MRT) cluster analyses) for each community cluster (A to F). CVRE: cross-validated relative error (see text for details).

Community cluster	Location	Indicator taxon		IndVal index				
		Order: Family	Taxon	Ward	MRT #1	MRT #2	MRT #3	MRT #4
A	Mackenzie Shelf (low salinity and sandy sectors)	Polychaeta: Nephtyidae	*Micronephthys* sp.	0.94	0.90	0.85	0.87	0.96
		Polychaeta: Paraonidae	*Levinsenia* sp.	0.80	0.67	0.61	0.61	0.78
		Polychaeta: Pectinariidae	*Cistenides* sp.	0.66	0.62	0.56	0.52	0.91
B	Mackenzie and Amundsen Gulf shelves (sandy sectors)	Polychaeta	Capitellidae	0.69	0.64	0.63	0.71	-
C	Mackenzie Shelf (highly silty and clayey sectors)	Polychaeta: Nephtyidae	*Bipalponephtys* sp.	0.99	0.49	0.80	0.87	0.91
		Cumacea: Leuconidae	*Leucon* sp.	0.89	0.65	0.71	0.79	0.84
		Bivalvia	Galeommatoidea	0.86	-	0.76	0.78	0.67
		Gastropoda	*Cylichna* sp.	0.77	-	0.67	0.74	0.66
D	Beaufort Sea and Amundsen Gulf (shelf break)	Polychaeta: Opheliidae	*Ophelina* sp.	0.59	0.63	0.59	0.58	-
E	Beaufort Sea and Amundsen Gulf (slope)	Polychaeta: Maldanidae	*Maldane* sp.	0.80	0.76	0.76	0.74	0.80
		Polychaeta: Onuphidae	*Paradiopatra* sp.	0.69	0.67	0.68	0.64	0.73
		Polychaeta: Ampharetidae	*Amage* sp.	0.62	0.64	0.64	0.70	0.75
		Polychaeta: Ampharetidae	*Melinna* sp.	0.57	0.67	0.68	0.69	0.70
F	Beaufort Sea (deep slope)	Mollusca: Scaphopoda	*Siphonodentalium* sp.	0.81	0.75	0.81	0.90	0.89
		Sipuncula	Sipuncula	0.67	0.58	0.61	0.61	0.61
		Polychaeta: Nephtyidae	*Aglaophamus* sp.	0.62	0.58	0.57	0.62	0.63
		Tanaidacea	*Pseudosphyrapus* sp.	0.52	0.44	0.53	-	0.61
		Polychaeta: Pilargidae	*Sigambra* sp.	0.42	0.39	0.43	0.48	0.48
			No. of communities	6	5	6	6	7
			R^2	-	0.19	0.23	0.29	0.37
			CVRE	-	0.87	0.84	0.79	0.78

DISCUSSION

This study determined environmental predictors of spatial macrofaunal patterns (richness, density and community composition) in the southeastern Beaufort Sea and Amundsen Gulf regions based on the aggregation of all data available from 1973 to 2012. We discuss the relative importance of the different environmental variables retained in the best-solution models in regards to their spatial scale of variability (regional or sub-regional variability). Finally, we validate our initial hypothesis of low temporal variability and discuss other methodological considerations regarding our models.

Environmental predictors of macrofaunal patterns

Regional patterns

Environmental variables retained in predictive models of both univariate biodiversity metrics (richness, density) and multivariate community composition (communities) were primarily depth and bottom water physical properties (salinity, temperature) rather than sediment characteristics, as we hypothesized and as other Arctic studies have demonstrated (Denisenko *et al.* 2003; Carroll *et al.* 2008; Cochrane *et al.* 2009; Carroll & Ambrose 2012). These abiotic factors vary over the entire breadth of the study area and are correlated with the regional macrofaunal patterns. Changes in community composition coincided with the environmental gradient of increasing bottom water salinity and temperature from the shallowest stations on the Mackenzie and Amundsen Gulf shelves to the deepest areas of the Beaufort Slope and central Amundsen Gulf. The strong relationship of depth and bottom water physical properties with the spatial distribution of macrofaunal communities over sub-regional differences was also reported by Conlan *et al.* (2008). For instance, at similar depths, a similar macrofaunal community may be found in the most western part of the study area in Mackenzie Trough and in the most eastern part in Amundsen Gulf (e.g., communities D and E, Figure 25). Across the study area, the transition between the main water masses (Pacific to Atlantic) overlapped with the shelf break as both occurred around 200 m depth (Carmack & MacDonald 2002; O'Brien *et al.* 2006). In this context, teasing apart the relative importance of bottom water physical properties, depth and topography in structuring macrofaunal patterns is challenging. Influence of water masses on distributional patterns of invertebrate larvae may be important (Metaxas 2001), but we lack information on potential drivers of larval dispersion and recruitment in the study area. In addition, different physiological tolerances of benthic organisms may explain the role of water properties on benthic richness and community composition (Levin *et al.* 2001). Additional studies are needed to elucidate the relative importance of bottom water physical properties versus depth on macrobenthos patterns.

Increase in depth across the study area could be regarded at the same time as a vertical gradient of decreasing food availability and as a horizontal gradient of increasing distance from coastal and riverine influence. Richness and density were lowest near the Mackenzie Delta and at the deepest stations (> 500 m) of the study area. The freshwater and sediment load discharges of the Mackenzie River could induce several disturbances to the benthos in the inner sector of Mackenzie Shelf by means of the variation in salinity, temperature, and turbidity. Furthermore, the inshore is subject to regular ice scour disturbance within the 8-35 m depth range (Blasco *et al.* 1998; Carmack & MacDonald 2002). However, small scale patterns induced by ice scouring were not measurable in this study, which was large scale in scope and did not include stations in the most active zone of ice scouring around the 20 m isobath. The observed spatial pattern of heavier surface sediment $\delta^{13}C$ values towards deep stations reflected the decreasing importance of terrestrial organic matter over marine organic matter supply in driving the composition of sedimentary organic carbon. The fate of terrigenous carbon in Arctic benthic food webs remains poorly understood but it is generally considered of low quality for benthos (Klages *et al.* 2004). Across the study area, surface sediments are in fact dominated by refractory terrigenous and marine components (Magen *et al.* 2010). We therefore interpreted the relationships of heavier sediment $\delta^{13}C$ with decreasing richness and density observed in our models through the indirect influence of depth on all these variables. Sediment $\delta^{13}C$ was not retained in predictive models of community composition. In this case the decreasing amount of food reaching the deepest stations had likely more impact on the distribution of communities than had the composition of the sedimentary organic carbon. On Arctic shelves, the strongest attenuation of vertical particulate organic carbon (POC) flux may be very important in the first 50 m due to the rapid biological consumption and remineralization of carbon (Carmack & Wassmann 2006). As depth increases, generally only a small fraction of the net primary production in the euphotic zone reaches deep benthic communities (Smith *et al.* 2008). For instance, only about 5 % of the surface POC reached 210 m water depth in the central area of Amundsen Gulf over a three-year assessment (Forest *et al.* 2010), in agreement with the low macrofaunal densities that we observed. Meiobenthos also showed patterns of decreasing abundance and biomass with increasing depth across the study area (Bessiere *et al.* 2007). Consequently, we believe that strong vertical POC flux attenuation likely caused, along with the vertical water mass gradient, the clear depth zonation of macrofaunal patterns across the study area.

Sub-regional patterns

Sediment grain size variation (shown here as % sand) was a good secondary environmental driver when added in univariate and multivariate models. High silt and clay content characterized globally the surface sediments of the study area with few stations having high (> 50 %) sand content, as reported by other studies (Conlan *et al.* 2008; Conlan *et al.* 2013; Jerosch 2013). The proportion of sand varied more on the shelf (< 200 m) than in deeper sectors (≥ 200 m), and thus reflected mostly a sub-regional scale of variation specific to erosion by bottom current on the shelf that exposes older beach deposits (Jerosch 2013) and to artificial sand islands (Conlan *et al.* 2013). Substrate variability profoundly affects benthic community structure in all marine systems due to specific requirements of benthic organisms from larval to adult stages (Snelgrove & Butman 1994). Indicator taxa of communities A and B, i.e., the polychaetes *Micronephthys* sp., *Levinsenia* sp., *Cistenides* sp. and Capitellidae, were associated with relatively low salinity and sandy silt and clay sediments on the shelf. These latter taxa were also reported as abundant on the shelf by Conlan *et al.* (2008) and appeared to be favoured by estuarine conditions. The spatially restricted community C located in silt and clay-rich sediments on the middle

Mackenzie Shelf appeared to be less favoured by estuarine conditions and sandy sediments than communities A and B, and was characterized by the polychaete *Bipalponephtys* sp., the cumacean *Leucon* sp., the bivalve Galeommatoidea, and the gastropod *Cylichna* sp. Communities A and C were almost exclusively observed on the Mackenzie Shelf, but additional sampling on the narrow shelf of Amundsen Gulf region are needed to elucidate the sub-regional distinctiveness of these latter communities. The communities located off the shelf (i.e., D, E and F) were all associated with muddy sedimentary environments and their distinctiveness between each other could be associated with the shelf break and slope topography and/or with a gradient of decreasing food supply with depth. Among the indicator taxa of the deep communities, the polychaetes *Ophelina* sp., *Maldane* sp., *Melinna* sp., and the members of the phylum Sipuncula, were also reported by Conlan *et al.* (2008) as more abundant in off shelf areas than on the shelf. These latter taxa are known to be deposit feeders (Fauchald & Jumars 1979) and they are presumably well adapted to low food supply.

The area of high macrofaunal biomass spreading west of Cape Bathurst (estimated at 4550 km^2) defined by Conlan *et al.* (2013) was again well delimited in the present study with the highest richness and density found in that area. A combination of steep topography and episodic wind-driven upwelling brings nutrient-rich Pacific water onto the shelf around and to the northwest of Cape Bathurst (Williams & Carmack 2008). This nutrient enrichment has positive consequences across the food web, from primary producers (Tremblay *et al.* 2011) to zooplankton (Walkusz *et al.* 2012) and benthos (Conlan *et al.* 2008; Conlan *et al.* 2013; Roy *et al.* 2014), and to higher trophic levels, such as marine birds (Dickson & Gilchrist 2002), bowhead whales (Walkusz *et al.* 2012) and gray whales (Conlan *et al.* 2013). The Mackenzie Trough is also an area of upwelling (Williams *et al.* 2006) coincident with high macrofaunal richness and density that we observed on the shelf surrounding it, as well as high biomass reported by Conlan *et al.* (2013). While these upwelling areas have a great influence on bulk macrofaunal density and biomass, we did not observe in these upwelling areas distinctive sub-regional community clusters. This difference reflects that recurrent and elevated food supply at sub-regional scale produce primarily a footprint on the benthos abundance, in terms of bulk density or biomass, with negligible influence on the community composition. Sediment organic carbon and sediment pigments have been successfully correlated with macrofaunal richness, density and biomass in several Arctic studies (Carroll *et al.* 2008; Cochrane *et al.* 2009; Carroll & Ambrose 2012), but they were poor environmental predictors in the present study. Sediment pigments are often regarded as 'food supply proxies' of short-term variability due to their rapid degradation and are therefore well correlated with short-term benthic responses, such as benthic oxygen demand (Renaud *et al.* 2007b; Link *et al.* 2011; Link *et al.* 2013a). Sediment organic carbon has a higher temporal integration than sediment pigments (Morata *et al.* 2008), but both had high localized spatial variability which makes them less appropriate descriptors in the context of this study considering the spatial and temporal extents of the data sets.

Temporal variability and methodological considerations

Our key hypothesis is that the temporal variability across the different sampling programs over 1973-2012 was negligible considering the well-established long-term integrative responses of offshore macrofaunal communities to their environment (Pearson & Barnett 1987; Clarke & Warwick 2001). In agreement with our hypothesis, we demonstrated that mean density and community composition were not significantly different among the three time periods considered (i.e., 1973-1975, 2002-2004 and 2007-2012) for the depth range overlapped by the threes (i.e., 31-441 m depth range). Mean richness was lower in the CASES (2002-2004) data set than in the historical (1973-1975) data set, but this difference was rather small and we do not consider it sufficient to be related to temporal variability. This slight difference may result in part from the variable area sampled per station, the homogenisation of faunal data sets, and also in part from the different spatial coverage of each data set. Low temporal variability at the spatial scale of our study was also reported in other Arctic studies (e.g., northern Bering Sea (Dunton *et al.* 2005); Barents Sea (Carroll *et al.* 2008); Chukchi Sea (Blanchard & Feder 2013)), and also in extra-polar areas (e.g., Gulf of Mexico (Wei *et al.* 2012)). In the Canadian Arctic, Cusson *et al.* (2007) showed that the temporal variability in benthic densities was of the same order as spatial variability at rather small scales only (a few kilometers) and suggested that large scale patterns may be less affected by environmental changes over time. Across our study area, Conlan et al. (2008) similarly found that community composition varied more with depth than time of sampling. Conlan *et al.* (2013) revealed a strong temporal concordance in the macrofaunal biomass data collected at the Cape Bathurst shelf edge between 2000's data and data collected nearly 30 years before (Wacasey 1975; Wacasey *et al.* 1977), thus suggesting that physical-biological conditions did not change broadly over this period.

To aggregate and homogenize all faunal data sets together, we had to scale some taxa at higher levels of taxonomic resolution. It has been shown that choosing a lower level of taxonomic resolution did not compromise the outcome of benthic community analysis for most Canadian Arctic regions (Cusson *et al.* 2007). The close environment-biota relationships that we found here suggest that using genus as the lowest level of taxonomic resolution did not impede the performance of our models. This latter consideration along with the low temporal variability that we observed and the relatively long-term stability of the primary abiotic factors retained in all predictive models strengthens our recommendation to consider the spatial macrofaunal patterns that we observed as a regional baseline state for evaluating future temporal and spatial macrofaunal variations.

Both univariate and multivariate predictive models performed well with % of variance explained that are typical for biological systems (Cottenie 2005) because the latter are influenced by highly complex interactions between both biotic and abiotic factors that are not always available to be included in models (Moller & Jennions 2002). Biotic factors such as competition, predation and recruitment are rarely included in Arctic studies (e.g., Conlan and Kvitek 2005) due to logistic constraints in studying recurrently the same communities, especially in offshore areas. The proportion of variance explained by all predictive models increased from data subset #1 to #4, partly due to the decreasing ratio of the number of stations relative to the number of explicative factors entered in the models

(Legendre & Legendre 1998) and also to the increasingly smaller size of the data sets. We do not propose consequently to use necessarily the regression equations and the MRT community clusters associated with data subset #4 purely based on the fact that they had the greatest proportion of variance explained. We rather propose that the unique inclusion of bottom water physical properties, depth and sediment grain size, as used in data subset #2, should give appropriate resolution of the gradient in richness and density and of the discontinuities between the communities at the scale of the Beaufort Sea and Amundsen Gulf regions. In situations where a more localized modelling objective is intended, the present models should be used with caution, however, because the relative influence of environmental predictors might change with the spatial and temporal scale of investigation. We could expect that variables indicative of the amount and quality of food supply should have higher predictive influence at finer spatial scales and greater temporal resolution.

CONCLUSION

Our predictive models provide insights on the spatial gradients and driving abiotic factors of macrofaunal richness, density and community composition across the southeastern Beaufort Sea and Amundsen Gulf regions. All available environmental variables that were known to be influential on marine benthic communities and measured over 1973-2012 at the time of faunal collection were considered in this study. Bottom water physical properties and depth varied broadly over the scale of the study area and were the strongest predictors of macrofaunal patterns. In sub-regions (< 200 m) of the Mackenzie Shelf and Amundsen Gulf, sediment grain size variability also correlated with macrofaunal patterns. Sediment organic carbon and sediment pigments were poor predictors due presumably to their temporal variability over the time period considered and due to their spatial patchiness. We also acknowledge that other yet unavailable environmental variables should be considered in future studies, such as current velocity and annual estimates of POC flux near the seafloor. Future field programs in this region should continue to collect at least the same environmental variables that we used to increase the spatial data density and to build long time-series data that will be useful in the face of the rapid natural and anthropogenic changes that this region may encounter in upcoming decades.

We conclude that the insignificant seasonal variability and insignificant differences between the collecting programs along with the good performance of our models provide a coherent picture of the spatial distribution of macrofaunal richness, density and communities for evaluating future natural and anthropogenic induced impacts in this region. Our models may help decision-makers to elaborate guidelines and priorities for adequate conservation of habitats hosting specific communities in order to minimize or avoid impacts of anthropogenic disturbances, such as in defining Ecologically and Biologically Significant Areas (EBSAs) (Cobb *et al.* 2014). The environment-biota relationships found at the scale of the present study might also help scientists monitoring the spatial and temporal variation of macrofaunal patterns and help build more comprehensive models that aim at predicting macrofaunal diversity in areas of the Arctic where no faunal data have been collected.

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Appendix 3.

List of the top 5 significant indicator taxa for each community cluster (A to F), following the unconstrained cluster analysis (Ward's minimum variance) and four constrained cluster analyses (Multivariate Regression Tree - MRT). In **bold** are the indicator taxa that were common to at least four cluster analyses over five. CVRE: cross-validated relative error (see text for details).

		Unconstrained clustering		MRT #1		MRT #2		MRT #3		MRT #4	
Community cluster	Location	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index
A (or AB for MRT #1)	Mackenzie Shelf (low salinity and sandy sectors)	***Micronephthys* sp.**	0.94	***Micronephthys* sp.**	0.90	***Micronephthys* sp.**	0.85	***Micronephthys* sp.**	0.87	***Micronephthys* sp.**	0.96
		***Levinsenia* sp.**	0.80	*Macoma* sp.	0.68	***Levinsenia* sp.**	0.61	***Levinsenia* sp.**	0.61	***Cistenides* sp.**	0.91
		***Cistenides* sp.**	0.66	***Levinsenia* sp.**	0.67	Cirratulidae	0.58	*Scaphander* sp.	0.53	***Levinsenia* sp.**	0.78
		Macoma sp.	0.59	Capitellidae	0.64	***Cistenides* sp.**	0.56	***Cistenides* sp.**	0.52	*Scaphander* sp.	0.71
		Cirratulidae	0.58	***Cistenides* sp.**	0.62	Aricidea	0.53	Aricidea	0.51	Aricidea	0.61
B	Mackenzie Shelf and Amundsen Gulf shelf (sandy sectors)	**Capitellidae**	0.69	-	-	**Capitellidae**	0.63	*Astarte* sp.	0.78	*Bathyarca* sp.	0.62
		Diastylis sp.	0.67	-	-	*Diastylis* sp.	0.60	**Capitellidae**	0.71	*Ophiocten* sp.	0.57
		Ophiocten sp.	0.63	-	-	*Nuculana* sp.	0.56	*Praxillella* sp.	0.63	*Astarte* sp.	0.46
		Akanthophoreus sp.	0.59	-	-	*Astarte* sp.	0.50	*Nuculana* sp.	0.62	*Chone* sp.	0.45
		Ektonodiastylis sp.	0.59	-	-	*Scoloplos* sp.	0.49	*Akanthophoreus* sp.	0.60	*Pleurogonium* sp.	0.41
BB (only MRT #4)	Mackenzie Shelf (specific sector for MRT #4)	-	-	-	-	-	-	-	-	*Anonyx* sp.	0.67
		-	-	-	-	-	-	-	-	*Eugerda* sp.	0.62
		-	-	-	-	-	-	-	-	*Scoloplos* sp.	0.62
		-	-	-	-	-	-	-	-	Lysianassidae	0.62
		-	-	-	-	-	-	-	-	*Pholoe* sp.	0.59
C (or BC for MRT #1)	Mackenzie Shelf (highly silty and clayey sectors)	***Bipalponephtys* sp.**	0.99	***Leucon* sp.**	0.65	***Bipalponephtys* sp.**	0.80	***Bipalponephtys* sp.**	0.87	***Bipalponephtys* sp.**	0.91
		***Leucon* sp.**	0.89	*Eudorella* sp.	0.59	**Galeommatoidea**	0.76	***Leucon* sp.**	0.79	***Leucon* sp.**	0.84
		Galeommatoidea	0.86	*Ophiocten* sp.	0.59	Holothuroidea	0.73	**Galeommatoidea**	0.78	Leuconidae	0.75
		Leuconidae	0.77	Holothuroidea	0.50	***Leucon* sp.**	0.71	Holothuroidea	0.75	**Galeommatoidea**	0.67
		***Cylichna* sp.**	0.77	***Bipalponephtys* sp.**	0.49	***Cylichna* sp.**	0.67	***Cylichna* sp.**	0.74	***Cylichna* sp.**	0.66

		Unconstrained clustering		MRT #1		MRT #2		MRT #3		MRT #4	
Community cluster	Location	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index	Indicator taxon	IndVal index
D	Beaufort Sea and Amundsen Gulf (shelf break)	*Pholoe* sp.	0.69	*Prionospio* sp.	0.65	**_Ophelina_ sp.**	0.59	*Ektonodiastylis* sp.	0.61	*Calathura* sp.	0.61
		Prionospio sp.	0.68	**_Ophelina_ sp.**	0.63	*Thyasira* sp.	0.59	*Syllis* sp.	0.59	*Syllis* sp.	0.61
		Thyasira sp.	0.62	*Thyasira* sp.	0.61	*Prionospio* sp.	0.57	**_Ophelina_ sp.**	0.58	*Paraphoxus* sp.	0.59
		Ampharete sp.	0.60	*Scoletoma* sp.	0.58	*Syllis* sp.	0.57	*Pholoe* sp.	0.55	*Myriochele* sp.	0.59
		Ophelina sp.	0.59	*Syllis* sp.	0.57	*Ektonodiastylis* sp.	0.56	*Calathura* sp.	0.54	*Ektonodiastylis* sp.	0.58
E	Beaufort Sea and Amundsen Gulf (slope)	**_Maldane_ sp.**	0.80	**_Maldane_ sp.**	0.76	**_Maldane_ sp.**	0.76	**_Maldane_ sp.**	0.74	**_Maldane_ sp.**	0.80
		Paradiopatra sp.	0.69	**_Paradiopatra_ sp.**	0.67	**_Paradiopatra_ sp.**	0.68	**_Amage_ sp.**	0.70	*Schistomeringos* sp.	0.77
		Nicomache sp.	0.66	**_Melinna_ sp.**	0.67	**_Melinna_ sp.**	0.68	**_Melinna_ sp.**	0.69	**_Amage_ sp.**	0.75
		Amage sp.	0.62	**_Amage_ sp.**	0.64	*Nicomache* sp.	0.64	**_Paradiopatra_ sp.**	0.64	**_Paradiopatra_ sp.**	0.73
		Melinna sp.	0.57	*Nicomache* sp.	0.59	**_Amage_ sp.**	0.64	*Schistomeringos* sp.	0.61	**_Melinna_ sp.**	0.70
F	Beaufort Sea (deep slope)	**_Siphonodentalium_ sp.**	0.81	**_Siphonodentalium_ sp.**	0.75	**_Siphonodentalium_ sp.**	0.81	**_Siphonodentalium_ sp.**	0.90	**_Siphonodentalium_ sp.**	0.89
		Sipuncula	0.67	**_Aglaophamus_ sp.**	0.58	**Sipuncula**	0.61	**_Aglaophamus_ sp.**	0.62	**_Aglaophamus_ sp.**	0.63
		Aglaophamus sp.	0.62	**Sipuncula**	0.58	**_Aglaophamus_ sp.**	0.57	**Sipuncula**	0.61	**_Pseudosphyrapus_ sp.**	0.61
		Pseudosphyrapus sp.	0.52	**_Pseudosphyrapus_ sp.**	0.44	**_Pseudosphyrapus_ sp.**	0.53	**_Sigambra_ sp.**	0.48	**Sipuncula**	0.61
		Sigambra sp.	0.42	**_Sigambra_ sp.**	0.39	**_Sigambra_ sp.**	0.43	*Chauliopleona* sp.	0.44	**_Sigambra_ sp.**	0.48
No. of communities		6		5		6		6		7	
R^2		-		0.19		0.23		0.29		0.37	
CVRE		-		0.87		0.84		0.79		0.78	

CHAPITRE 4
RÉPONSES DU RÉSEAU TROPHIQUE BENTHIQUE À LA PRODUCTION BIOLOGIQUE ET À LA PROFONDEUR DANS L'ARCTIQUE CANADIEN

RÉSUMÉ

Les voies d'assimilation de la matière organique des organismes benthiques, ainsi que la variation de la structure du réseau trophique benthique ont été étudiées le long de gradients de profondeur et de régimes de production biologique sur 2 000 km de l'Arctique canadien à l'aide de l'analyse de la composition des isotopes stables du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$). Trois sources potentielles de nourriture disponible au moment de l'échantillonnage (sédiment de surface et matière organique particulaire dans la colonne d'eau) et plus de 75 espèces benthiques appartenant à quatre guildes trophiques ont été analysées à 19 stations en 2011. La variabilité spatiale du $\delta^{13}C$ de la matière organique particulaire était liée à la biomasse phytoplanctonique au moment de l'échantillonnage, alors que la variabilité spatiale du $\delta^{13}C$ du sédiment de surface reflétait l'origine terrestre et marine de la matière organique. À la grandeur de l'aire d'étude, les valeurs en $\delta^{13}C$ des invertébrés benthiques étaient en moyenne plus élevées de 6.6 ‰ par rapport aux sources potentielles de nourriture. Les valeurs en $\delta^{13}C$ des invertébrés benthiques montraient plutôt un chevauchement étroit avec les valeurs isotopiques d'algues de glace répertoriées dans la littérature pour la même zone d'étude. De plus, la variabilité spatiale des valeurs en $\delta^{13}C$ des invertébrés benthiques était en lien avec les régions où les plus fortes biomasses d'algues de glace ont été répertoriées dans l'Arctique canadien, c'est-à-dire les détroits de Barrow et d'Éclipse. Aux stations profondes, les valeurs en $\delta^{15}N$ des consommateurs benthiques primaires indiquaient une assimilation de matière organique dégradée et les prédateurs-charognards benthiques avaient principalement une diète omnivore comparativement à leurs homologues sur le plateau continental. Cette étude démontre

l'importance actuelle des algues de glace en tant que source principale de carbone pour les communautés benthiques et suggère que la structure du réseau trophique benthique change le long du gradient de profondeur de l'Arctique canadien.

Ce quatrième article, intitulé « *Benthic food-web responses to marine biological productivity and depth across the Canadian Arctic* » fut corédigé par moi-même, ainsi que les professeurs Katrin Iken, Michel Gosselin, Jean-Éric Tremblay, Simon Bélanger et Philippe Archambault. L'article a été soumis le 24 juillet 2014 à la revue *Deep-Sea Research Part I.* En tant que première auteur, ma contribution à ce travail fut l'idée originale du projet, l'essentiel de la recherche bibliographique, l'échantillonnage, les analyses de laboratoire, le traitement statistique des résultats et la rédaction de l'article. Les professeurs K. Iken et M. Gosselin ont aidé à la définition de la problématique ainsi qu'à la révision de l'article. Les professeurs P. Archambault, J.-E. Tremblay et S. Bélanger ont aidé à la révision de l'article. Spécialisée dans l'utilisation des isotopes stables en écologie polaire, madame K. Iken m'a accueillie dans son laboratoire à l'hiver 2013 et m'a supervisée dans l'interprétation des résultats. Une version abrégée de cet article a été présentée à *l'Assemblée générale annuelle de Québec-Océan* à Rivière-du-Loup (Canada) à l'automne 2013, ainsi qu'à la conférence *Ocean Sciences Meeting* à Honolulu (États-Unis) à l'hiver 2014.

BENTHIC FOOD-WEB RESPONSES TO MARINE BIOLOGICAL PRODUCTIVITY AND DEPTH ACROSS THE CANADIAN ARCTIC

ABSTRACT

The organic matter assimilation pathways of benthic organisms, along with food-web structure, were investigated at shelf and slope locations spanning 2000 km across the Canadian Arctic using stable carbon and nitrogen isotope analysis. Three potential food sources and over 75 benthic taxa belonging to four feeding guilds were analyzed, but the $\delta^{13}C$ end-members for the benthic food-webs could not be clearly discerned. While spatial patterns of $\delta^{13}C$ for pelagic particulate organic matter were linked to phytoplankton biomass at the time of sampling, sediment $\delta^{13}C$ values reflected the relative composition of terrestrial and marine organic matter. On average, benthic primary consumers were enriched in ^{13}C by 6.6 ‰ compared to the potential organic matter sources sampled in the water column and sediment. The $\delta^{13}C$ discrepancy between identified sources of organic matter and benthic organisms suggests that an uncharacterised food source provided a significant carbon source to these animals. We propose that the ^{13}C enrichment of benthic organisms was largely caused by the assimilation of ice algae, particularly in regions of known high ice-algal standing stock such as Barrow Strait and Eclipse Sound. The $\delta^{15}N$ values of bottom-water particulate organic matter and of benthic primary consumers increased with depth due to greater degradation of the settling organic material. The $\delta^{15}N$ values of secondary consumers did not increase with depth, leading to a decrease of their trophic position compared with shallower regions and likely reflecting an increase in omnivory due to scarcity of prey at depth. This study emphasizes the importance of sea-ice algae as a carbon source for benthic communities in the Canadian Arctic and suggests that distinct food-web structures prevail over the shelf and slope.

***Keywords*:** stable isotopes, benthos, food web, Arctic, marine biological productivity, sea-ice algae, depth.

INTRODUCTION

Marine benthic shelf and slope ecosystems of the world's oceans rely mostly on the delivery to the seafloor of food produced in the euphotic zone. In polar environments, benthic communities can be sustained by direct sedimentation of sea-ice associated algae and phytoplankton cells and/or through the sinking of organic material processed by pelagic secondary consumers (e.g., fecal pellets, carcasses of animals; Piepenburg 2005). Pelagic algal production represents the largest fraction of annual primary production in Arctic waters with ice algal production contributing only 3 to 30 % (Carmack *et al.* 2006). The strength of pelagic-benthic coupling and the relative importance of these carbon sources in the diet of Arctic benthic communities are influenced by many environmental and ecological factors. For instance, when the release of ice algae is sudden or when phytoplankton blooms sink abruptly and pelagic grazers are scarce, the vertical export of particulate organic matter (POM) may be efficiently delivered to the benthos, especially over the shallow continental shelves that characterize the Arctic (Tremblay *et al.* 2006a). As water depth increases, however, benthic communities become subject to increased food limitation as the amount and quality of sinking POM through the water column is limited by processes in pelagic heterotrophic food webs (e.g., Mintenbeck *et al.* 2007; Smith *et al.* 2008; Bergmann *et al.* 2009). Despite high temporal variability in particle flux, the labile POM reaching the sediment of polar systems may persist for a long time and thus provide a long-term sediment 'food bank' for the benthic communities (Mincks *et al.* 2005).

Pelagic-benthic coupling strength and its impact on benthic trophic structure is reasonably well understood for certain shallow shelf regions of the Arctic, such as the northern Bering and Chukchi seas (e.g., Dunton *et al.* 1989; Lovvorn *et al.* 2005; Iken *et al.* 2010; McTigue & Dunton 2013) and the Barents Sea/Svalbard Archipelago (e.g., Tamelander *et al.* 2006a; Søreide *et al.* 2013; Carroll *et al.* 2014), but less so for deep Arctic regions (Iken *et al.* 2005; Bergmann *et al.* 2009), the Beaufort Sea (Dunton *et al.* 2006) and the Canadian Archipelago. For the latter, which represents a substantial fraction of the total Arctic Ocean area, current knowledge of POM assimilation pathways in shelf and slope benthic ecosystems is rudimentary and limited to only two regional-scale studies of the Barrow Strait-Lancaster Sound area (Hobson & Welch 1992) and the North Water (NOW) polynya (Hobson *et al.* 2002). In the face of a rapidly changing Arctic and anticipated impacts on the sympagic and pelagic primary production regimes and on benthic communities (Bluhm & Gradinger 2008), there is a growing need to establish a large-scale reference baseline of the major organic carbon sources currently sustaining Canadian Arctic benthic communities. The highly diverse bathymetry and productivity regimes that defines the Canadian Arctic (Ardyna *et al.* 2011) makes it an excellent area to explore spatial variability in benthic food-web responses.

To elucidate the pathways by which POM is biologically processed and passed on to higher trophic levels, it is useful to explore the functional role of different organismal groups as it relates to their functional morphology or feeding mode. Since benthic primary consumers such as suspension and surface deposit feeders rely on different particle sizes (Mintenbeck *et al.* 2007, and references therein) and secondary consumers may express different predatory and omnivorous feeding habits (Thompson *et al.* 2007; Thompson *et al.* 2009), their trophic responses along environmental gradients (e.g., marine primary production, depth) can be used to elucidate how environmental forcing of food supply acts on the composition and distribution of benthic communities. The ultimate carbon sources of consumers can be traced using carbon stable isotope ratio ($\delta^{13}C$) if they have distinct $\delta^{13}C$ signatures, since fractionation per trophic step (i.e. the consistent, stepwise enrichment exhibited by stable isotopes during biological processing) is small for carbon (0-1 ‰; Peterson & Fry 1987; Vander Zanden & Rasmussen 2001; Post 2002). For example, sea-ice algae are enriched in ^{13}C on average by 4-5 ‰ compared to phytoplankton (Hobson *et al.* 2002; Tamelander *et al.* 2006a; Carroll *et al.* 2014), so their distinctive $\delta^{13}C$ signatures may serve as a tracer of the main carbon source in consumer tissues of seasonally ice-covered polar systems. Nitrogen stable isotope ratios ($\delta^{15}N$), on the other hand, are used to assess the mean trophic position of organisms in a food web because the enrichment step in ^{15}N between source and consumer is relatively large (3-4 ‰; Peterson & Fry 1987; Vander Zanden & Rasmussen 2001; Post 2002).

The main objective of this study was to investigate POM assimilation pathways for different benthic primary and secondary consumer guilds, and to assess if and how their carbon and nitrogen stable isotope compositions and food-web structure vary spatially across marine productivity and depth regimes of the Canadian Arctic. We specifically addressed the following research questions: (1) Is the spatial variability in the isotopic signatures of the potential food sources and trophic guilds driven by the same environmental variables?, (2) Are the carbon isotopic signatures of primary benthic consumers similar to available food sources at the time of sampling (pelagic-POM and surface sediment) or to other uncharacterised food source (e.g., sea-ice algae)?, and (3) Does the nitrogen isotopic signature of different trophic guilds respond to depth, therefore reflecting a change in food-web structure? We hypothesized that (i) different environmental factors explain the spatial variability in potential food sources and trophic guilds, and (ii) the marine productivity gradient (sea-ice algal or pelagic algal production) will mostly govern $\delta^{13}C$ variability of potential food sources and trophic guilds while depth will drive their $\delta^{15}N$ variability.

MATERIALS AND METHODS

Study area

This study was conducted across the Canadian Arctic from the southeastern Beaufort Sea in the west (129°W) to Baffin Bay in the east (70°W), including stations throughout the Archipelago (Figure 27). The Beaufort Sea and Amundsen Gulf regions in the western study region are highly influenced by the Mackenzie River that drains a 1.7 x 10^6 km^2 watershed and discharges approximately 340 km^3 y^{-1} of freshwaters (McLaughlin *et al.* 2004) and 127 x 10^6 Mt y^{-1} of sediment (Macdonald *et al.* 2004) into the Beaufort Sea. Two main water masses are layered through the Canadian Arctic, with the warmer-saline Atlantic-origin waters on the bottom of the region (on average > 200 m depth) and the colder-fresher Pacific-origin waters directly above (on average < 200 m depth) (McLaughlin *et al.* 2004). The complex topography of the Archipelago with its numerous islands and channels has a profound influence on sea ice dynamics and marine biological productivity. During winter the study area is ice-covered and sea ice could be found throughout the summer as landfast ice or first-year and multiyear pack ice (Howell *et al.* 2009; EC 2010). Summer sea ice distribution along with ice break-up and freeze-up dates exhibit large inter-annual variations (Howell *et al.* 2009; EC 2010). Following a general trend, ice stays longer in summer in the central part of the Canadian Arctic Archipelago than in western and eastern parts where large and latent heat polynyas open in spring, such as the North Water (NOW), Lancaster Sound-Bylot Island (LS-BI), and the Cape Bathurst (CB) polynyas (Michel *et al.* 2006; Howell *et al.* 2008) (Figure 27). Accordingly, field-based and satellite-derived observations of pelagic primary production (PP) are higher in NOW, LS-BI and CB polynyas than in the central, ice-covered part of the Canadian Arctic Archipelago (Ardyna *et al.* 2011; Bélanger *et al.* 2013). The study area was divided into three geographical regions (west, center and east) (Figure 27) in order to test for the effects of spatial gradients in ice trends and biological productivity on benthic communities.

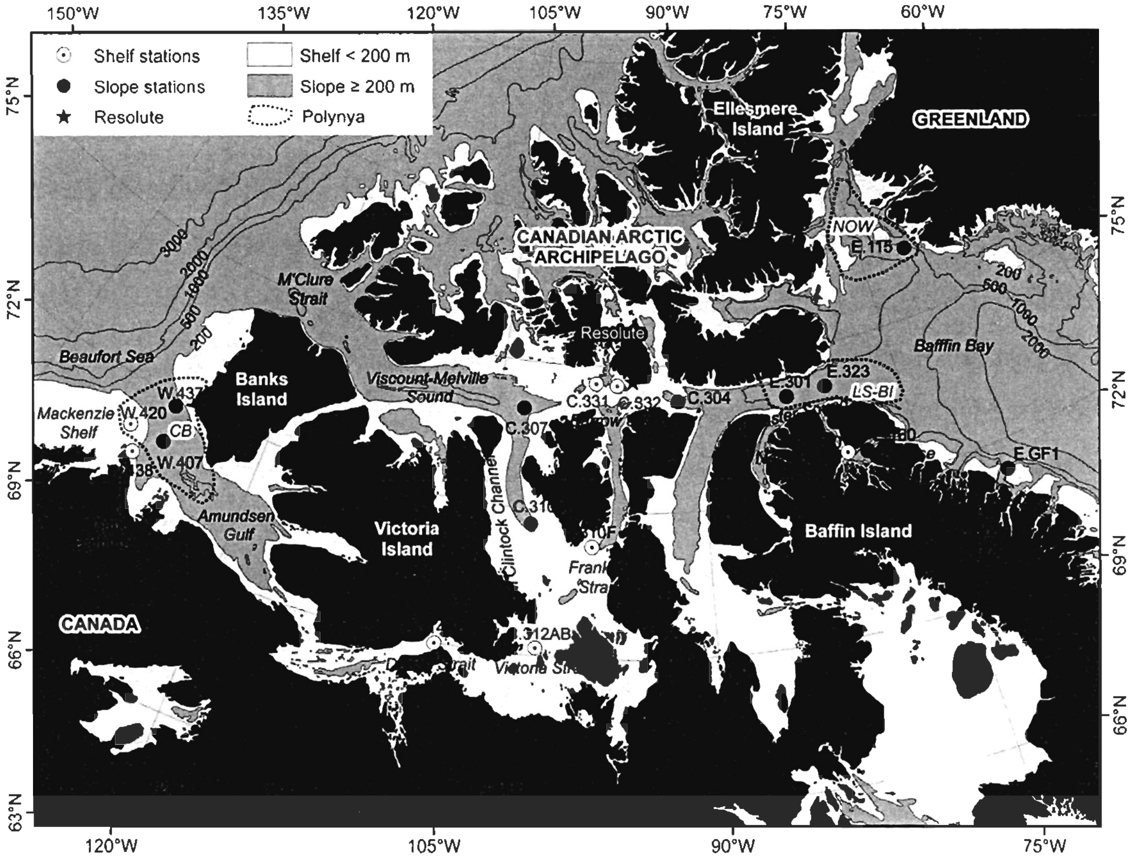

Figure 27. Location of the 19 stations sampled from August to October 2011 across the Canadian Arctic. Stations are grouped in three regions following average sea ice conditions (W: west, C: center, E: east). Symbols represent stations on the shelf (< 200 m; white dotted circles) and slope (≥ 200 m; black circles); AB: stations sampled twice in A: August and B: October 2011. Main polynyas are indicated by dotted polygons and by capital italic letters (*CB*: Cape Bathurst polynya, *LS-BI*: Lancaster Sound-Bylot Island polynya, *NOW*: North Water polynya; based on Arrigo and van Dijken 2004 and Barber and Massom 2007).

Field sampling

A total of 19 stations were sampled between August and October 2011 onboard the Canadian research icebreaker CCGS *Amundsen* (Figure 27; Table 13). Two stations were sampled both in August and October to assess seasonal variability in stable isotope composition (stations 312AB and 314AB, Figure 27). Sampling station depths ranged from 35 to 789 m. Stations were split in two depth categories (shelf < 200 m: n = 8; slope ≥ 200 m: n = 11) with the shelf break assumed to be around 200 m (O'Brien *et al.* 2006; Spalding *et al.* 2007) (Figure 27).

At each station, a CTD-Rosette was deployed to collect water samples at various depths (defined below) using 12 L Niskin-type bottles to determine stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of suspended POM and to measure chlorophyll *a* (Chl *a*) concentration. POM from the subsurface chlorophyll maximum layer (SCM-POM) and from 10 m above bottom (Bot-POM) were sampled from the same CTD cast. Replicates were not possible at each station. On average 10 L were filtered onto pre-combusted (450 °C for 5 h) 47 mm diameter Whatman GF/F glass-fiber filters (nominal pore size 0.7 μm). Visible zooplankton swimmers on the filters were removed. All POM filters were kept at -80 °C until drying at 60 °C for 48 h. Size-fractionated Chl *a* concentrations (≥ 0.7 μm and ≥ 5 μm) were measured at 7 optical depths (from surface to 0.2 % surface light level), including the SCM depth, using the methods described in detail in Ardyna *et al.* (2011). Due to the late sampling season, sea-ice algal production could not be measured.

At each station, a USNEL box corer (0.25 m^2) was deployed to collect seafloor sediments for the determination of stable isotope composition and pigment (Chl *a* + phaeopigments) concentrations. From each box core, surface sediments (upper 1 cm) were sampled as three sub-cores using a 60 ml disposable syringe (2.6 cm diameter with a cut off anterior end). Sediment samples were immediately frozen at -20 °C for stable isotope analysis and at -80 °C for pigment analysis.

Table 13. Station location, bottom oceanographic variables and marine productivity proxies. Station codes correspond to ArcticNet expedition labels; stations are ordered by depth categories (shelf and slope) and geographical regions (W: west, C: center, E: east).

		Spatial variable			Bottom oceanographic variable		
Station code	Sampling date	Lat. (°N)	Long. (°W)	Bottom depth (m)	Salinity	Temp. (°C)	Diss. oxygen (ml l^{-1})
Shelf (< 200 m)							
W.420	26-Sep	71.050	-128.520	35	31.65	-0.87	9.43
W.438	29-Sep	70.588	-127.613	94	33.32	-1.33	6.39
C.314A	10-Aug	68.995	-106.620	109	28.82	-1.41	7.99
C.314B	06-Oct	69.000	-106.559	119	28.82	-0.81	8.65
C.312A	09-Aug	69.173	-100.755	70	30.30	-1.22	8.01
C.312B	07-Oct	69.169	-100.706	66	29.86	-0.21	8.46
C.310F	08-Aug	71.299	-97.604	165	32.92	-1.18	5.58
C.331	03-Aug	74.636	-97.733	113	32.60	-1.35	6.54
C.332	04-Aug	74.600	-96.116	143	32.71	-1.23	6.20
E.150	01-Aug	72.739	-79.921	130	33.19	-1.36	7.03
Slope (≥ 200 m)							
W.437	28-Sep	71.828	-126.505	239	34.65	0.13	6.01
W.407	02-Oct	71.074	-126.180	408	34.83	0.40	6.72
C.310M	07-Oct	71.693	-101.706	200	34.24	-0.45	4.92
C.307	08-Oct	74.021	-103.062	368	34.79	0.37	4.93
C.304	12-Oct	74.253	-91.502	315	33.84	-0.15	5.57
E.301	14-Oct	74.094	-83.417	665	34.52	1.54	4.97
E.323	15-Oct	74.147	-80.454	789	34.51	1.31	4.82
E.160	01-Aug	72.670	-78.577	726	34.39	1.07	4.79
E.115	17-Oct	76.330	-71.146	647	34.37	0.38	6.07
E.GF1	20-Oct	71.404	-70.115	364	34.24	0.92	5.68
E.GF2	21-Oct	70.760	-72.268	448	34.06	0.41	5.35

Table 13 continued.

		Marine productivity proxy										
		≥ annual		≤ annual	Seasonal							
Station code	Sampling date	PP 5Y (g C m^{-2} 5y^{-1})	PP 1Y (g C m^{-2} y^{-1})	Sed. pigments (µg g^{-1})	SCM B_T (µg l^{-1})	SCM B_S (µg l^{-1})	SCM B_L (µg l^{-1})	SCM B_L:B_T	Euphotic B_T (mg m^{-2})	Euphotic B_S (mg m^{-2})	Euphotic B_L (mg m^{-2})	Euphotic B_L:B_T
Shelf (< 200 m)												
W.420	26-Sep	129.24	30.40	5.24	0.72	0.49	0.23	0.32	14.01	9.09	4.91	0.35
W.438	29-Sep	na	na	5.26	0.80	0.57	0.23	0.29	21.25	12.90	8.35	0.39
C.314A	10-Aug	41.00	8.83	7.89	3.07	0.24	2.83	0.92	120.42	13.93	106.49	0.88
C.314B	06-Oct	41.00	8.83	12.40	0.37	0.31	0.07	0.18	16.54	12.57	3.98	0.24
C.312A	09-Aug	26.83	6.37	8.72	7.82	1.22	6.60	0.84	146.90	11.68	135.21	0.92
C.312B	07-Oct	26.53	6.32	19.86	0.50	0.28	0.21	0.43	26.61	13.83	12.78	0.48
C.310F	08-Aug	30.92	4.94	2.76	20.87	3.42	17.45	0.84	281.96	45.21	236.75	0.84
C.331	03-Aug	57.43	10.56	4.47	8.09	0.49	7.60	0.94	287.11	16.76	270.35	0.94
C.332	04-Aug	54.73	11.57	23.32	5.77	0.19	5.58	0.97	348.76	24.62	324.15	0.93
E.150	01-Aug	24.07	3.63	2.13	0.64	0.40	0.24	0.38	22.96	9.29	13.67	0.60
Slope (≥ 200 m)												
W.437	28-Sep	48.24	11.00	2.58	0.44	0.36	0.09	0.20	25.12	20.28	4.83	0.19
W.407	02-Oct	64.95	14.86	2.87	0.79	0.00	0.79	1.00	29.42	23.75	5.66	0.19
C.310M	07-Oct	20.42	3.75	2.16	0.39	0.31	0.08	0.22	19.23	11.49	7.74	0.40
C.307	08-Oct	12.34	2.78	1.75	2.79	0.86	1.93	0.69	75.20	16.62	58.58	0.78
C.304	12-Oct	78.60	11.20	57.67	3.78	0.94	2.85	0.75	153.18	41.27	111.91	0.73
E.301	14-Oct	79.67	12.83	36.43	0.58	0.11	0.47	0.81	38.71	13.04	25.67	0.66
E.323	15-Oct	97.32	18.12	21.31	0.16	0.05	0.11	0.67	35.02	10.43	24.59	0.70
E.160	01-Aug	22.54	3.59	12.83	0.37	0.16	0.21	0.56	13.13	5.65	7.48	0.57
E.115	17-Oct	162.23	26.15	12.39	0.57	0.38	0.19	0.34	19.81	14.23	5.58	0.28
E.GF1	20-Oct	73.69	9.34	7.95	0.65	0.35	0.30	0.46	33.94	21.70	12.24	0.36
E.GF2	21-Oct	na	na	5.96	0.42	0.34	0.08	0.19	21.51	16.84	4.67	0.22

PP: satellite-derived phytoplankton production integrated over a period of 1 or 5 years before sampling; SCM: subsurface chlorophyll maximum; euphotic: down to 0.2 % of surface light; B_T: total phytoplankton biomass (cells ≥ 0.7 µm); B_S: biomass of small phytoplankton cells (0.7–5 µm); B_L: biomass of large phytoplankton cells (≥ 5 µm); B_L:B_T: relative contribution of large phytoplankton cells to total biomass; na: data not available.

Megabenthic invertebrates were principally collected with an Agassiz trawl (effective opening of 1.5 m and a net mesh size of 40 mm, with a 5 mm cod end liner) with average trawling time and speed of 5 min and 1.5 knots, respectively. At three stations, invertebrates were collected with the box corer (C.331, C.332 and C.314A; Figure 27). Trawl and box corer catches were washed over a 2 mm sieve under running sea water onboard and 1 to 3 individuals of the most abundant community representatives were collected at each station (Roy *et al.* 2014). Specimens were frozen immediately at -80 °C and identified to the lowest possible taxonomic level in the lab.

Near-bottom water temperature (°C), salinity and dissolved oxygen concentration (ml l^{-1}) were determined at each station by the shipboard CTD Seabird™ profiler (SBE911 Plus), combined with a SBE 43 dissolved oxygen sensor, 10 m above the seafloor.

Sample preparation and stable isotope analysis

Stable isotope analyses were performed on different potential food sources available at the time of sampling (i.e., pelagic-POM (including SCM-POM and Bot-POM) and sediment) and on benthic fauna.

Food sources

Pelagic-POM samples for organic carbon content and stable carbon isotopic composition ($\delta^{13}C$) determination were acidified in order to remove inorganic carbon. SCM-POM and Bot-POM samples were processed in two labs (see also below in Analysis sub-section). SCM-POM filters were soaked once or twice for 1 h in 150 µl of 1 N HCl (Université Laval, Canada), and Bot-POM filters were placed in a desiccator saturated with HCl fumes for 24 h (Université du Québec à Rimouski, Canada). Nitrogen content and stable nitrogen isotopic composition ($\delta^{15}N$) were determined on untreated samples.

Surface sediment organic carbon content and $\delta^{13}C$ was determined after acidification with 1 N HCl whereas nitrogen content and $\delta^{15}N$ were determined on untreated samples. In recent studies on Arctic Ocean sediments (e.g., Schubert & Calvert 2001; Kuzyk *et al.*

2009; Kuzyk *et al.* 2010), the C_{ORG}/N_{TOT} molar ratio was corrected to C_{ORG}/N_{ORG} molar ratio to account for the presence of bound inorganic nitrogen. We corrected for the presence of inorganic nitrogen by subtracting the positive N-intercept value from a regression of N_{TOT} vs. C_{ORG} ($N_{TOT} = 0.0256 + 0.1007\ C_{ORG}$, $r^2 = 0.93$). Uncorrected and corrected sediment C/N molar ratios are presented for comparison in Table 14. Only corrected C/N molar ratios were used in subsequent data analyses. The C/N molar ratios and stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) were used to outline the spatial variation of sedimentary POM composition (marine vs. terrigenous) across the study area. We retrieved from the literature the most extreme end-member values available for Canadian Arctic sediments: a terrigenous end-member in the terrestrially-influenced Beaufort Sea region ($\delta^{13}C$ = -27 ‰ and C/N = 10 to 20; Macdonald *et al.* 2004) and a 98 % marine derived end-member from Hudson Bay ($\delta^{13}C$ = -20.4 ‰, C/N = 7.5; Kuzyk *et al.* 2010).

Ice-POM stable isotope values were used for comparisons with the above food sources and with benthic fauna. Ice-POM $\delta^{13}C$ and $\delta^{15}N$ values (bottom 3-10 cm of ice cores) were retrieved from the literature for the Beaufort Sea/Amundsen Gulf region (Pineault *et al.* 2013) and the NOW polynya (Tremblay *et al.* 2006b). We also used data collected in Resolute Passage from 8 May to 15 June 2010 and collected in Allen Bay from 27 April to 16 June 2011 (M. Gosselin and C.J. Mundy, unpublished data).

Benthic fauna

We selected muscle and/or structural tissues (exoskeleton) of benthic organisms to represent a mid- to long-term tissue turnover (Mateo *et al.* 2008) to explore the spatial variability in benthic food-web dynamics in response to long-lasting and/or recurrent environmental conditions. Replicate individuals of benthic taxa were sub-sampled for muscle tissue, and/or pieces of body wall when muscle tissue could not be distinguished. Foot and adductor muscle tissues were selected for bivalves; upper part of the central disc for ophiuroids; tube feet for large sea stars and an arm section for small sea stars; abdomen and telson with the exoskeleton for arthropods; posterior body part for annelids; and whole organism for hydrozoan and bryozoan taxa. Sub-sampled muscle tissues were then dried at

60 °C for at least 24 h. Prior to stable isotope analysis, all faunal sub-samples were lipid-extracted using chloroform-methanol (2:1 by volume). The tissue-solvent mixture was sonicated for 5 min, then centrifuged for 5 min and the supernatant discarded. This extraction procedure was repeated three times. Lipids were removed from all samples to reduce the variability attributed to differences in lipid content across tissues and because lipids are relatively depleted in ^{13}C (Tamelander *et al.* 2006a; Mateo *et al.* 2008). Samples that contained carbonates (i.e., echinoderms, arthropods, calcified bryozoans and hydrozoans, and some bivalves with remaining sediments) were treated with 1 N HCl until bubbling ceased, and then dried at 60 °C for at least 48 h. Acidified samples were not rinsed with water to avoid removal of acid-soluble proteins (Mateo *et al.* 2008). Nitrogen isotopic composition of taxa that contained carbonates was determined on non-acidified aliquots because acidification may alter $\delta^{15}N$ values (Mateo *et al.* 2008). We determined $\delta^{15}N$ of tissues that did not contain carbonates (i.e., bivalves and polychaetes) on lipid-extracted tissues, after testing on various untreated samples ($n = 52$) that the solvent mixture slightly changed $\delta^{15}N$ values by 0.8 ‰ on average, a value largely inferior to the assumed 3.4 ‰ enrichment in $\delta\ ^{15}N$ between successive trophic levels (Vander Zanden & Rasmussen 2001; Post 2002).

Analysis

Elemental composition (C and N) and stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) were measured by continuous flow isotope ratio mass spectrometry (CF-IRMS). One quarter of each filter (SCM-POM and Bot-POM), about 5 mg of sediment and 1 mg of invertebrate samples were analysed. Analyses for SCM-POM were carried out using an ECS 4010 elemental analyzer (Costech Analytical Technologies Inc.) coupled with a Delta V Advantage IRMS (Thermo Electron Corporation) (Université Laval, Canada). Analyses for Bot-POM, sediment and invertebrate samples were performed using an ECS 4010 elemental analyzer (Costech Analytical Technologies Inc.) coupled with a Delta$^{\text{Plus}}$ XP IRMS (Thermo Electron Corporation) at the Marine Chemistry and Mass Spectrometry Laboratory (Université du Québec à Rimouski, Canada). Replicate measurements of international standards (USGS40 and USGS 41 from the International Atomic Energy Agency; B2151 from Elemental Microanalysis) gave measurement errors of ± 0.1 ‰ for $\delta^{13}C$ and ± 0.2 ‰ for $\delta^{15}N$ at both laboratories. Replicate measurements of international standards or internal biological standards were used to calibrate the systems and compensate for drift over time. Parallel analyses on five random split pelagic-POM filters were carried out at the two laboratories and revealed slight differences that were mostly within the range of measurement errors (mean differences of ± 0.1 ‰ for $\delta^{13}C$ and ± 0.9 ‰ for $\delta^{15}N$).

Stable isotope ratios are expressed in delta (δ) notation (in ‰) relative to international standards (Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen) according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Trophic level

Pelagic-POM has been used in several studies as the food-web baseline (e.g., Iken *et al.* 2005; Tamelander *et al.* 2006a; Bergmann *et al.* 2009), but the large seasonal variability in POM isotopic signature can complicate cross-system comparisons of food-web structure. An alternative approach is to use the mean $\delta^{15}N$ value of specialized primary consumers as the food-web baseline (Post 2002; Vander Zanden & Fetzer 2007). We selected only SF taxa as baseline among all the primary consumers available in this study, because specialized primary consumers are advantageous to avoid variation due to the high variability in feeding modes of benthic primary deposit feeders (Dunton *et al.* 1989; Iken *et al.* 2010). Food-web structure was compared between the two depth categories, shelf ($<$ 200 m) and slope ($\geq$ 200 m), using selected suspension feeder taxa (SF) that were available across the depth range of the study area (bryozoans and ampeliscid amphipods) as baseline. Shelf SF taxa were *Alcyonidium* spp., *Ampelisca macrocephala* and *Haploops laevis*; slope SF taxa were *Alcyonidium* spp. and *Ampelisca eschrichtii* (Appendix 4). Trophic levels (TL) of consumers were determined using the equation:

$$TL = [(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{selected SF}})/3.4] + 2$$

where 3.4 is the assumed average enrichment in $\delta^{15}N$ between successive TL (Vander Zanden & Rasmussen 2001; Post 2002). $\delta^{15}N_{\text{selected SF}}$ refers to the mean $\delta^{15}N$ values of the selected SF taxa for each depth category.

Marine productivity proxies

To link spatial variations of $\delta^{13}C$ and $\delta^{15}N$ values in food sources and in benthic invertebrates with spatial variations of marine biological productivity, we used various marine productivity proxies in surface waters, surface sediment and sea ice. These productivity proxies exhibited spatial variation over different scales of temporal variability (see below).

Surface waters

We evaluated the influence of phytoplankton production on the isotopic signature of SCM-POM at the time of sampling using field-measurement of Chl *a* concentrations at the SCM depth. We related the phytoplankton production integrated over the euphotic zone (from surface to 0.2 % surface light level) with the isotopic signature of Bot-POM. The influence of cell size was also tested because large cells sink rapidly and are assumed to contribute substantially to the carbon reaching the seafloor (Wassmann 1998). Based on Chl *a* concentrations, we calculated the following size-fractionated phytoplankton biomass: euphotic B_T = total phytoplankton biomass (cells ≥ 0.7 µm; mg Chl *a* m^{-2}); euphotic B_S = biomass of small phytoplankton cells (0.7–5 µm; mg Chl *a* m^{-2}); euphotic B_L = biomass of large phytoplankton cells (≥ 5 µm; mg Chl *a* m^{-2}); and euphotic B_L:B_T = relative contribution of large cells to total biomass.

We evaluated the long-term (≥ annual) influence of pelagic phytoplankton carbon production on isotopic signatures of benthic fauna and sediment using annual satellite-derived PP estimates. Satellite-derived Chl *a*, light attenuation, incident downwelling irradiance and sea ice concentration were used to estimate monthly PP in open waters following Bélanger *et al.* (2013) approach. Briefly, daily PP rates were calculated using a fully spectral model that uses as input (1) the monthly Chl *a* concentration and diffuse light attenuation coefficient derived from Sea Wide-Field-of-View (SeaWiFS, 1998-2010) or the Moderate Resolution Imaging Spectroradiometer (MODIS-aqua, 2011), (2) the 3-hours cloud cover thickness and extent from the International Satellite Cloud Climatology Project (ISCCP), and (3) the daily sea ice cover extent from the Special Sensor Microwave Imager (SSM/I) and the Special Sensor Microwave Imager Sounder (SSMIS) (for details see Bélanger et al. 2013). For the purpose of this study, the monthly estimates of PP were integrated over two periods of time prior faunal sampling to obtain a cumulative production of pelagic phytoplankton. All valid pixels within a radius of 20 km around each sampling station were averaged for given month and then integrated over one (PP 1Y) or five years (PP 5Y) before benthic sampling (data not available for stations W.438 and E.GF2).

Surface sediment

We evaluated the mid-term (≤ annual) influence of marine POM inputs to the seafloor on the isotopic signatures of benthic fauna and sediment using sediment total pigment concentration (Chl *a* + phaeopigments; µg pigment g^{-1} dry sediment). Sediment samples were analysed fluorometrically following a modified protocol by Riaux-Gobin and Klein (1993) (for details see Roy *et al.* 2014).

Sea ice

To assess regional variability in sea-ice algal biomass from field measurements, we retrieved maximal Chl *a* concentrations (bottom 3-10 cm of ice cores) that were available in four regions across the present study area. From west to east: Beaufort Sea/Amundsen Gulf (Pineault *et al.* 2013), Resolute Passage/Barrow Strait (Welch & Bergmann 1989), Eclipse Sound (Cross 1982) and NOW polynya (Tremblay *et al.* 2006b).

Data analysis

Based on literature, benthic organisms were assigned exclusively to one of the four following benthic feeding guilds: suspension feeders (SF), facultative suspension feeders/surface deposit feeders (SF/SDF), a combined group of surface deposit feeders and subsurface deposit feeders (SDF + SSDF), and predator-scavenger feeders (P/S) (Appendix 4). We considered the SF, SF/SDF and SDF + SSDF guilds as belonging to the broad group of primary consumers based on the definition that they feed on primary producer-derived POM, and we considered the P/S guild as secondary consumers. Although the SDF and SSDF guilds feed in separate sediment horizons, McTigue and Dunton (2013) observed in the northern Chukchi Sea that their sources of assimilated POM were equivalent.

Before undertaking the different parametric statistical tests, the normality of distribution was verified using Shapiro-Wilk test and the equality of variances was verified using *F*-test. When required, a logarithmic or square-root transformation was applied to the data. Student's *t*-tests were used to seek differences between the two depth categories (i.e., shelf and slope) and Welch correction was applied to estimate the degrees of freedom in case of heterogeneous variances (Welch 1938). Kruskal-Wallis tests were carried out to identify differences between the three geographical regions (west, center and east). When significant, these latter tests were completed by multiple comparison tests between regions using Bonferroni correction ($\alpha = 0.05$/number of comparisons). Pearson linear correlations with permutation tests were used to relate $\delta^{13}C$ and $\delta^{15}N$ of benthic feeding guilds and food sources to quantitative environmental variables (marine productivity proxies and spatial variables). Relationships between $\delta^{15}N$ values of benthic organisms grouped by benthic feeding guild and depth were modelled using simple linear regressions. All linear regression models were validated for following assumptions: normality of residuals was examined by plotting theoretical quantiles vs. standardized residuals (Q-Q plots) and homogeneity of variance was verified graphically by plotting residual vs. fitted (predicted) values. Possible outliers with severe influence on the models were identified using Cook's Distance (D), but none had $D > 1$ (Quinn & Keough 2002). To fulfill the assumption of independent observations in all statistical analyses, we established that the significant isotope August-to-October variability observed for both pelagic-POM components allowed us to consider pelagic-POM measurements made in August (stations C.312A and C.314A) and October (C.312B and C.314B) to be independent observations (statistical analyses on 21 stations). Surface sediment and benthic taxa exhibited low seasonal variability and, subsequently, measurements made in August were not considered independent from those in October; August measurements (stations C.312A and C.314A) were removed from statistical analyses performed on surface sediment and benthic feeding guilds (remaining $n = 19$ stations). All data were analyzed in the statistical package R version 3.0.1 (R Core Team 2013). A significant threshold of $\alpha = 0.05$ was adopted for all statistical tests.

RESULTS

Spatial and seasonal $\delta^{13}C$ and $\delta^{15}N$ variability in potential food sources

The three food sources (SCM-POM, Bot-POM and surface sediment) were depleted in ^{13}C on average by 6.5 ‰ compared to Ice-POM $\delta^{13}C$ values recorded previously in three regions covered by the present study area (Figure 28a, Table 14). Food source $\delta^{15}N$ values were, however, similar to the range of Ice-POM $\delta^{15}N$ values (Figure 28b). No significant differences in $\delta^{13}C$ and $\delta^{15}N$ were detected among the three geographical regions for SCM-POM and Bot-POM (Table 15). Significantly higher Bot-POM $\delta^{15}N$ were measured at slope stations than at shelf stations, and the opposite was observed for Bot-POM $\delta^{13}C$ (Table 15). Surface sediment $\delta^{13}C$ and $\delta^{15}N$ values were significantly lower in the west than in the center of the study area and were not significantly different between shelf and slope stations (Table 15).

Three potential food sources were collected twice at two stations on the shelf, in summer (August) and fall (October) 2011, to assess seasonal $\delta^{13}C$ and $\delta^{15}N$ variability (stations C.312AB and C.314AB; Figure 27). We visually detected meaningful differences (> 1 ‰; i.e., variation beyond analytical precision), because insufficient replicates were available for statistical analysis for each food source and/or benthic taxa (Figure 29). SCM-POM and Bot-POM $\delta^{13}C$ values were more enriched in ^{13}C from 2.0 to 3.7 ‰ in summer than in fall (Figure 29a, b). Seasonal differences of less than 1 ‰ were observed for surface sediment $\delta^{13}C$ values (Figure 29a, b). For both pelagic-POM components, $\delta^{15}N$ seasonal differences were less than 1 ‰, except at station C.314AB where SCM-POM was more enriched in ^{15}N by 1.5 ‰ in summer than in fall (Figure 29c, d). Sediment $\delta^{15}N$ values were higher in fall than in summer by 1.3 ‰ (station C.312AB) and 1.6 ‰ (station C.314AB) (Figure 29c, d). The higher seasonal variability (mostly in $\delta^{13}C$) observed for SCM-POM and Bot-POM than for surface sediment caused us to test their relationships with marine productivity regimes using proxies integrating temporal variability at different scales. We related the stable isotope composition variability in (i) SCM-POM and Bot-POM with seasonal marine productivity proxies (Tables 1, 2), and (ii) variability in surface sediment with annual to multiannual marine productivity proxies (Tables 1, 2). Significant positive correlations showed that $\delta^{13}C$ and $\delta^{15}N$ variability in SCM-POM followed the variability in total phytoplankton biomass (SCM B_T) and the biomass and relative proportion of large phytoplankton cells ($\geq$ 5μm; SCM B_L and SCM B_L:B_T, respectively) (Table 16). The $\delta^{13}C$ variability in Bot-POM was positively correlated with the biomass and relative proportion of large phytoplankton cells when integrated over the euphotic zone (euphotic B_L and euphotic B_L:B_T; Table 16). Difference in $\delta^{13}C$ between SCM-POM and Bot-POM (Δ $\delta^{13}C$ SCM-Bot) was not related to phytoplankton biomass, but Δ $\delta^{15}N$ SCM-Bot was negatively correlated with the relative contribution of large phytoplankton cells integrated over the euphotic zone (euphotic B_L:B_T) (Table 16). Neither Bot-POM $\delta^{13}C$ nor Δ $\delta^{13}C$ SCM-Bot variability was related to depth. Depth had, however, a significant positive correlation with Δ $\delta^{15}N$ SCM-Bot (Table 16).

Surface sediment spatial $\delta^{13}C$ and $\delta^{15}N$ variability reflected the relative terrestrial and marine composition of sediment POM (Figure 30). Surface sediments at stations with a strong terrestrial signal were depleted in ^{13}C and ^{15}N and had high C/N molar ratio, while sediment at stations with a high marine POM source showed opposite trends. Surface sediment POM at two stations located on the Mackenzie Shelf was primarily of terrestrial origin (W.420 and W.438) and four stations with a mix of terrestrial and marine origin were located in Amundsen Gulf (W.407 and W.437), in Gibbs Fjord inlet (E.GF2), and in Navy Board Inlet (E.150). The remaining stations reflected mixed composition with a predominantly marine source. These latter stations exhibited a narrower range of $\delta^{13}C$ values (-23.9 to -22.2 ‰) relative to the large range of $\delta^{15}N$ values (5.8 to 11.1 ‰) and C/N values (9.2 to 14.5 mol:mol). Surface sediment $\delta^{13}C$ values were positively correlated with sediment pigments and latitude and surface sediment $\delta^{15}N$ values were negatively correlated with PP 1Y, PP 5Y and latitude (Table 17).

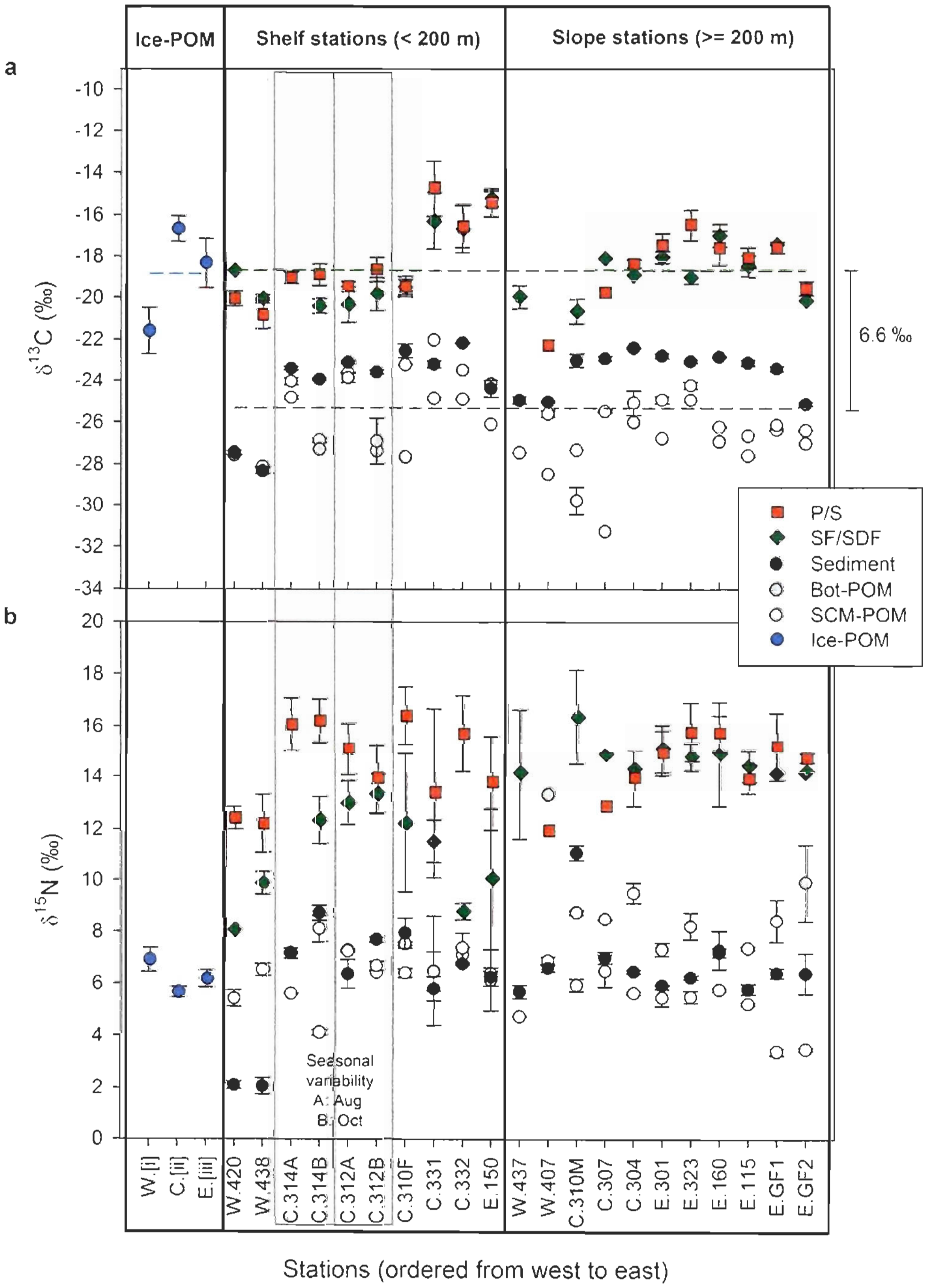
Ice-POM
Shelf stations (< 200 m)
Slope stations (>= 200 m)
a
b
δ^{13}C (‰)
δ^{15}N (‰)
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
-32
-34
20
18
16
14
12
10
8
6
4
2
0
6.6 ‰
P/S
SF/SDF
Sediment
Bot-POM
SCM-POM
Ice-POM
Seasonal variability
A: Aug
B: Oct
W.[i]
C.[ii]
E.[iii]
W.420
W.438
C.314A
C.314B
C.312A
C.312B
C.310F
C.331
C.332
E.150
W.437
W.407
C.310M
C.307
C.304
E.301
E.323
E.160
E.115
E.GF1
E.GF2
Stations (ordered from west to east)

Figure 28. Depth and geographic variations in (**a**) $\delta^{13}C$ and (**b**) $\delta^{15}N$ for three potential food sources (SCM-POM, Bot-POM and surface sediment) and the two most common feeding guilds sampled across the study area (SF/SDF and P/S); SF and SDF + SSDF feeding guilds are not shown for clarity. (**a**) Dashed blue line: average $\delta^{13}C$ of Ice-POM data; dashed green line: average $\delta^{13}C$ of SF/SDF; dashed dark gray line: average $\delta^{13}C$ of the three food sources combined. Stations are ordered from west to east (W.: West, C.: Center, E.: East) within each depth category; AB: stations sampled twice in A: August and B: October 2011; Bot-POM was not available for stations W.437 and W.438; SCM-POM was at the same depth as Bot-POM at station W.420. Ice-POM data (blue circles): W.[i]: 2008 data in Amundsen Gulf (n = 15 sampling events) (Pineault *et al.* 2013); C.[ii]: 2010-2011 data in Allen Bay/Resolute Passage area (M. Gosselin and C.J. Mundy, unpublished data, n = 62); E.[iii]: 1998 data in NOW polynya (n = 21) (Tremblay *et al.* 2006b). Errors bars represent standard error of the mean.

Table 14. Mean (± SE) $\delta^{13}C$ and $\delta^{15}N$ values (‰) of three potential food sources (SCM-POM, Bot-POM, surface sediment). C/N molar ratios (mol:mol) are shown for surface sediment (with correction for the presence of bound inorganic nitrogen. Station codes correspond to ArcticNet expedition labels; stations are ordered by depth categories (shelf and slope) and geographical regions (W: west, C: center, E: east).

	Pelagic-POM						Surface sediment			
Station code	$\delta^{13}C$ SCM-POM	$\delta^{13}C$ Bot-POM	Δ $\delta^{13}C$ SCM-Bot	$\delta^{15}N$ SCM-POM	$\delta^{15}N$ Bot-POM	Δ $\delta^{15}N$ SCM-Bot	$\delta^{13}C$	$\delta^{15}N$	C_{ORG}/N_{TOT}	C_{ORG}/N_{ORG}[d]
Shelf (< 200 m)										
W.420	-27.6 ± 0.0[b]	-27.6 ± 0.0[b]	0.0	5.4 ± 0.3[b]	5.4 ± 0.3[b]	0.0	-27.4 ± 0.1[c]	2.1 ± 0.2[c]	9.6 ± 2.3[c]	18.2 ± 3.7[c]
W.438	-28.1 ± 0.0[b]	na	na	6.5 ± 0.2[b]	na	na	-28.3 ± 0.1[c]	2.1 ± 0.3[c]	13.5 ± 2.2[c]	19.2 ± 2.9[c]
C.314A	-24.8 ± 0.1[b]	-24.0 ± 0.2[b]	0.8	5.6 ± 0.0[b]	7.2 ± 0.0[b]	1.6	-23.4 ± 0.1[c]	7.2 ± 0.2[c]	8.3 ± 0.2[c]	9.9 ± 0.2[c]
C.314B	-26.9 ± 0.1[b]	-27.3[a]	0.4	4.1 ± 0.1[b]	8.1 ± 0.5[b]	4.0	-23.9 ± 0.1[c]	8.8 ± 0.3[c]	10.0 ± 0.1[c]	12.3 ± 0.2[c]
C.312A	-23.6 ± 0.0[b]	-23.8 ± 0.2[b]	0.2	7.3 ± 0.0[b]	7.3 ± 0.1[b]	0.0	-23.1 ± 0.1[c]	6.4 ± 0.6[c]	6.3 ± 2.0[c]	9.8 ± 3.3[c]
C.312B	-27.4[a]	-26.9 ± 1.1[b]	0.5	6.4[a]	6.7 ± 0.2[b]	0.3	-23.6 ± 0.1[c]	7.7 ± 0.1[c]	8.3 ± 0.8[c]	14.5 ± 1.3[c]
C.310F	-23.2 ± 0.0[b]	-27.6[a]	4.4	6.4 ± 0.2[b]	7.6 ± 0.1[b]	1.2	-22.5 ± 0.3[c]	8.0 ± 0.6[c]	8.1 ± 0.1[c]	13.6 ± 0.5[c]
C.331	-24.9 ± 0.1[b]	-22.0[a]	2.9	6.5 ± 2.1[b]	6.5 ± 0.8[b]	0.0	-23.2 ± 0.2[c]	5.8 ± 0.5[c]	7.0 ± 0.9[c]	9.2 ± 1.4[c]
C.332	-24.9 ± 0.0[b]	-23.5[a]	1.4	7.1 ± 0.3[b]	7.4 ± 0.6[b]	0.3	-22.2 ± 0.0[c]	6.8 ± 0.0[c]	8.8 ± 0.9[c]	9.9 ± 1.0[c]
E.150	-26.1[a]	-24.1[a]	2.0	6.4 ± 0.1[b]	6.2 ± 1.2[b]	0.2	-24.4 ± 0.4[c]	6.3 ± 0.4[c]	4.9 ± 0.3[c]	14.8 ± 4.4[c]

Table 14 continued.

Station code	Pelagic-POM						Surface sediment			
	$\delta^{13}C$ SCM-POM	$\delta^{13}C$ Bot-POM	Δ $\delta^{13}C$ SCM-Bot	$\delta^{15}N$ SCM-POM	$\delta^{15}N$ Bot-POM	Δ $\delta^{15}N$ SCM-Bot	$\delta^{13}C$	$\delta^{15}N$	C_{ORG}/N_{TOT}	C_{ORG}/N_{ORG}^{d}
Slope (≥ 200 m)										
W.437	-27.4 ± 0.0^b	na	na	4.7 ± 0.0^b	na	na	-24.9 ± 0.2^c	5.7 ± 0.3^c	9.5 ± 0.3^c	14.3 ± 1.2^c
W.407	-25.6 ± 0.2^b	-28.5^a	2.9	6.9 ± 0.2^b	13.3a	6.4	-25.0 ± 0.1^c	6.6 ± 0.2^c	9.3 ± 0.3^c	10.7 ± 0.4^c
C.310M	-27.3 ± 0.0^b	-29.8 ± 0.7^b	2.5	6.0 ± 0.2^b	8.8 ± 0.1^b	2.8	-23.0 ± 0.3^c	11.1 ± 0.3^c	7.6 ± 0.1^c	11.4 ± 0.5^c
C.307	-25.5 ± 0.1^b	-31.3^a	5.8	6.5 ± 0.6^b	8.5 ± 0.0^b	2.0	-22.9 ± 0.1^c	7.0 ± 0.2^c	6.7 ± 0.9^c	9.4 ± 1.8^c
C.304	-25.1 ± 0.6^b	-26.0^a	0.9	5.6 ± 0.0^b	9.5 ± 0.4^b	3.9	-22.4 ± 0.0^c	6.5 ± 0.1^c	10.1 ± 0.7^c	11.1 ± 0.8^c
E.301	-24.9 ± 0.2^b	-26.8^a	1.9	5.5 ± 0.3^b	7.4 ± 0.3^b	1.9	-22.8 ± 0.1^c	6.0 ± 0.0^c	10.3 ± 0.8^c	11.8 ± 1.0^c
E.323	-24.2 ± 0.2^b	-24.9^a	0.7	5.5 ± 0.2^b	8.2 ± 0.5^b	2.7	-23.0 ± 0.1^c	6.3 ± 0.1^c	11.1 ± 0.4^c	12.4 ± 0.5^c
E.160	-26.2 ± 0.0^b	-26.9^a	0.7	5.8 ± 0.1^b	7.3 ± 0.7^b	1.5	-22.8 ± 0.0^c	7.2 ± 0.2^c	10.8 ± 0.3^c	13.1 ± 0.4^c
E.115	-27.6 ± 0.1^b	-26.6^a	1.0	5.2 ± 0.1^b	7.4 ± 0.1^b	2.2	-23.1 ± 0.1^c	5.8 ± 0.2^c	10.9 ± 1.6^c	12.3 ± 1.9^c
E.GF1	-26.4 ± 0.1^b	-26.1^a	0.3	3.4 ± 0.1^b	8.4 ± 0.8^b	5.0	-23.4 ± 0.1^c	6.4 ± 0.2^c	7.6 ± 0.7^c	9.9 ± 1.0^c
E.GF2	-26.4 ± 0.0^b	-27.0^a	0.6	3.5 ± 0.1^b	9.9 ± 1.5^b	6.4	-25.1 ± 0.1^c	6.4 ± 0.8^c	6.6 ± 0.7^c	12.6 ± 1.9^c

POM: particulate organic matter; SCM: subsurface chlorophyll maximum; Bot: 10 m above the seafloor; Δ SCM-Bot: stable isotope fractionation between SCM-POM and Bot-POM; na: data not available; ^{a}n = 1 sample; ^{b}n = 2 samples; ^{c}n = 3 samples. ^{d}Estimated by subtracting positive N_{TOT} intercept at $C_{ORG} = 0$ from all N_{TOT} values (see text for details).

Table 15. Student's *t*-test results for significant differences (> or <) between depth categories (shelf and slope) and between geographical regions (west, center and east) for the $\delta^{13}C$ and $\delta^{15}N$ of three food sources (SCM-POM, Bot-POM, surface sediment) and for two benthic feeding guilds (SF/SDF and P/S) shown in Figure 28. Gray cells indicate differences that were not biologically relevant to test; ns: not significant.

	Depth (shelf and slope)		Geographical region (west, center and east)	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Food source				
SCM-POM			ns	ns
Bot-POM	shelf > slope	shelf < slope	ns	ns
Sediment	ns	ns	west < center	west < center
Benthic feeding guild				
SF/SDF	ns	shelf < slope	ns	ns
P/S	ns	ns	west < east	ns

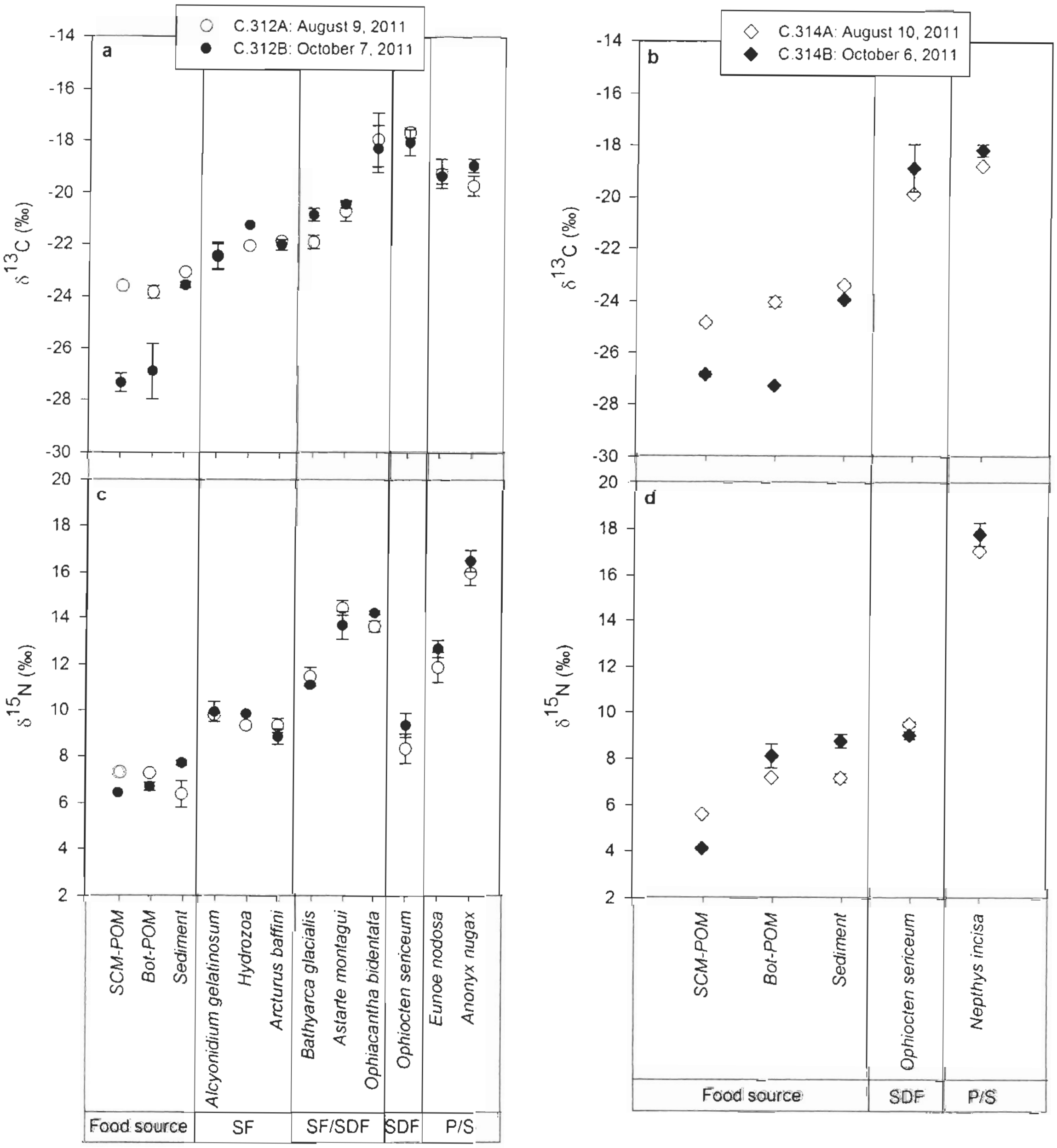

Figure 29. Seasonal variation at station C.312AB located in Victoria Strait (filled circles) and station C.314AB located in Dease Strait (filled diamonds). (**a-b**) $\delta^{13}C$ and (**c-d**) $\delta^{15}N$ for three potential food sources (SCM-POM, Bot-POM and surface sediment) and benthic taxa from different feeding guilds (SF, SF/SDF, SDF and P/S) sampled in August (white symbols) and October (black symbols) 2011. Errors bars represent standard error of the mean.

Table 16. Pearson linear correlation coefficients relating mean $\delta^{13}C$ and $\delta^{15}N$ of pelagic POM sampled at two depths (SCM-POM; Bot-POM) to seasonal marine productivity proxies and spatial variables (latitude and longitude starting at the most southwestern station) at 21 stations. Significant correlations ($p < 0.05$; 999 permutations) are indicated in **bold**; gray cells indicate correlations that were not biologically relevant to test.

	Pelagic-POM					Marine productivity proxy								Spatial variable		
	$\delta^{13}C$ SCM-POM	$\delta^{13}C$ Bot-POM	$\Delta\delta^{13}C$ SCM-Bot	$\delta^{15}N$ SCM-POM	$\delta^{15}N$ Bot-POM	SCM B_T	SCM B_S	SCM B_L	SCM $B_L:B_T$	Euphotic B_T	Euphotic B_S	Euphotic B_L	Euphotic $B_L:B_T$	Latitude	Longitude	Depth
$\delta^{13}C$ SCM-POM	1.00					**0.64**	0.34	**0.75**	**0.81**					0.13	0.24	
$\delta^{13}C$ Bot-POM	0.39	1.00								0.46	-0.03	**0.49**	**0.51**	0.09	0.23	-0.24
$\Delta\delta^{13}C$ SCM-Bot			1.00							0.39	0.39	0.38	0.32	0.37	-0.06	0.15
$\delta^{15}N$ SCM-POM	0.36			1.00		**0.52**	0.17	**0.59**	**0.58**					0.10	-0.34	
$\delta^{15}N$ Bot-POM		-0.40		-0.12	1.00					-0.06	0.43	-0.20	-0.38	-0.04	-0.07	0.42
$\Delta\delta^{15}N$ SCM-Bot										-0.32	0.28	-0.43	**-0.56**	-0.02	0.25	**0.60**

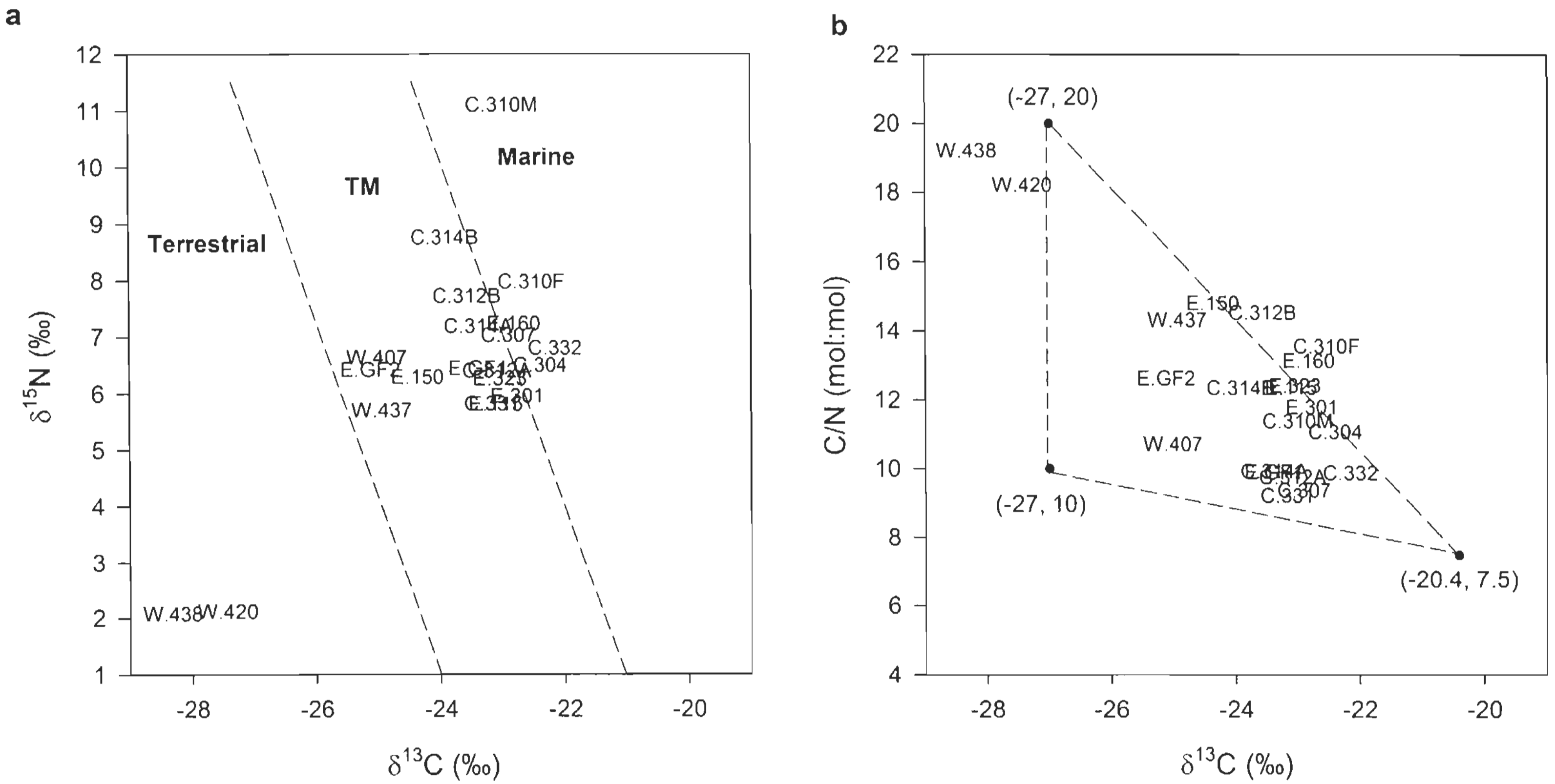

Figure 30. Surface sediment isotopic composition at 21 stations sampled between August and October 2011. (**a**) $\delta^{15}N$ versus $\delta^{13}C$; dashed lines represent Parsons' delineating lines (Parsons *et al.* 1989) for terrestrial (T) and marine (M) origin. TM represents an area of mixing between terrestrial and marine origin. (**b**) C/N molar ratio versus $\delta^{13}C$; dashed lines approximate organic matter composition assuming a marine end-member of $\delta^{13}C$ = -20.4‰, C/N = 7.5 (Kuzyk *et al.* 2010) and a terrigenous end-member of $\delta^{13}C$ = -27 ‰ and C/N = 10 to 20 (Macdonald *et al.* 2004). Each label represents the mean of three replicates per station.

Table 17. Pearson linear correlation coefficients relating mean $\delta^{13}C$ and $\delta^{15}N$ of benthic feeding guilds (SF available at 9 stations; SF/SDF at 18 stations; SDF + SSDF at 13 stations; P/S at 17 stations) and surface sediment ($n = 17$ stations, excluding stations W.420 and W.438 with a strong terrestrial signal shown in Figure 30) to annual and multiannual marine productivity proxies and spatial variables (latitude and longitude starting at the most southwestern station). Significant correlations ($p < 0.05$; 999 permutations) are indicated in **bold**.

	Benthic feeding guild				Marine productivity proxy			Spatial variable		
	SF	SF/SDF	SDF + SSDF	P/S	PP 5Y	PP 1Y	Sed. pigments	Latitude	Longitude	Depth
$\delta^{13}C$										
SF	1.00				0.02	-0.04	0.20	0.33	0.50	0.50
SF/SDF	**0.88**	1.00			0.00	-0.09	0.01	**0.54**	0.40	0.09
SDF + SSDF	0.64	**0.85**	1.00		0.07	0.14	0.17	0.41	0.11	-0.26
P/S	0.54	**0.77**	**0.72**	1.00	-0.02	-0.15	0.27	**0.52**	**0.61**	0.08
Sediment	0.31	0.25	0.40	0.40	0.08	-0.05	**0.48**	**0.53**	0.31	0.09
$\delta^{15}N$										
SF	1.00				0.06	0.00	0.32	0.51	0.56	**0.91**
SF/SDF	0.43	1.00			-0.15	-0.29	0.10	0.17	0.45	**0.72**
SDF + SSDF	**0.80**	**0.60**	1.00		**0.66**	**0.73**	0.14	0.13	0.29	**0.82**
P/S	0.42	0.33	-0.28	1.00	-0.22	-0.31	0.44	-0.06	**0.57**	0.22
Sediment	-0.70	0.16	-0.41	0.49	**-0.57**	**-0.55**	-0.20	**-0.52**	-0.22	-0.37

Spatial $\delta^{13}C$ and $\delta^{15}N$ variability in benthic feeding guilds

Across all stations, the primary consumers SF/SDF were enriched in ^{13}C on average by 6.6 ‰ compared with the three potential food sources combined (Figure 28a, Table 18). Ice-POM $\delta^{13}C$ values recorded formerly in three regions covered by the present study area overlapped with $\delta^{13}C$ values of the primary consumers SF/SDF (Figure 28a).

Isotopic signatures of a set of identical benthic taxa collected in summer and fall 2011 at the same stations (C.312AB and C.314AB) were less than 1 ‰ different (within analytical precision) for both $\delta^{13}C$ and $\delta^{15}N$ (Figure 29). This allowed us to focus on the spatial variability rather than the seasonal variability. The three geographical regions (west, center, east) only had significantly lower P/S $\delta^{13}C$ values in the west than in the east (Table 15), also reflected in a positive correlation of $\delta^{13}C$ values of P/S with longitude (Table 17). In addition, there were positive correlations of $\delta^{13}C$ values of SF/SDF and P/S with latitude (Table 17). Furthermore, the spatial distribution of $\delta^{13}C$ values for all four benthic feeding guilds showed that they were enriched in ^{13}C towards the northeastern sector of the study area (Figure 31). This observed $\delta^{13}C$ geographical pattern in benthic feeding guilds was not linked to PP 1Y and PP 5Y geographical patterns, but to areas of maximal ice algal biomass (Figure 32). Two areas showed particularly strong overlapping patterns between the highest $\delta^{13}C$ values of primary consumers (SF, SF/SDF, SDF + SSDF) and secondary consumers (P/S) (Figure 31) and the highest maximal ice algal biomasses recorded in the Canadian Arctic (Figure 32): stations C.331 and C.332 in Resolute Passage/Barrow Strait and stations E.150 and E.160 in Eclipse Sound.

SF/SDF $\delta^{15}N$ values were significantly higher at slope stations than at shelf stations, while no significant depth difference was detected for P/S feeding guild (Table 15). Linear regressions of $\delta^{15}N$ values of primary consumers (SF, SF/SDF and SDF + SSDF) with depth were all significant, but not for secondary consumers (P/S) (Figure 33). These linear models for each feeding guild were not triggered by measurements of different taxa across the depth range of the study area; three taxa that were sampled across the depth range within three feeding guilds showed similar $\delta^{15}N$ variability with depth as the overall respective feeding guilds. These taxa were the SF bryozoans, *Alcyonidium* spp., the SF/SDF bivalves, *Astarte* spp. and the P/S polychaete, *Aglaophamus malmgreni* (Figure 33). No common SDF + SSDF taxon was sampled across the depth range of the study area to make that comparison.

Table 18. Mean (± SE) $\delta^{13}C$ and $\delta^{15}N$ values (‰) of benthic feeding guilds collected in 2011 across the Canadian Arctic. Trophic level (TL) based on selected suspension feeder taxa ($SF_{selected}$) for baseline calculations (see text for details). Station codes correspond to ArcticNet expedition labels; stations are ordered by depth categories (shelf and slope) and geographical regions (W: west, C: center, E: east).

Station code	SF feeding guild							SF/SDF feeding guild						
	$\delta^{13}C$	± SE	$\delta^{15}N$	± SE	TL	± SE	n	$\delta^{13}C$	± SE	$\delta^{15}N$	± SE	TL	± SE	n
Shelf (< 200 m)														
W.420	-20.1	0.2	8.9	0.5	2.1	0.2	3	-18.7	0.0	8.1	na	1.8	na	1
W.438	-21.9	0.5	8.6	0.2	2.0	0.1	7	-20.1	0.2	9.9	0.4	2.4	0.1	3
C.314A	na	na	na	na	na	na	na	na	na	na	na	na	na	na
C.314B	na	na	na	na	na	na	na	-20.4	0.3	12.3	0.9	3.1	0.3	3
C.312A	-20.8	1.3	9.7	0.2	2.3	0.1	4	-20.3	0.8	13.0	0.8	3.4	0.2	4
C.312B	-21.8	0.3	9.6	0.3	2.3	0.1	4	-19.8	0.8	13.3	0.7	3.3	0.3	3
C.310F	-18.9	na	10.2	na	2.5	na	1	-19.5	0.4	12.2	2.7	3.1	0.8	3
C.331	na	na	na	na	na	na	na	-16.3	1.3	11.5	0.8	2.9	0.2	3
C.332	na	na	na	na	na	na	na	-16.7	1.1	8.8	0.3	2.0	0.2	2
E.150	na	na	na	na	na	na	na	-15.3	0.4	10.1	2.7	2.4	0.8	2
Slope (≥ 200 m)														
W.437	na	na	na	na	na	na	na	-20.0	0.6	14.1	2.5	2.2	0.7	4
W.407	-21.7	0.5	12.4	2.5	1.7	0.7	2	na	na	na	na	na	na	na
C.310M	-23.4	na	8.2	na	0.5	na	1	-20.7	0.6	16.3	1.8	2.9	0.5	2
C.307	na	na	na	na	na	na	na	-18.1	0.0	14.9	na	2.4	na	1
C.304	-21.4	na	10.3	na	1.1	na	1	-18.9	0.0	14.3	na	2.3	na	1
E.301	na	na	na	na	na	na	na	-18.1	0.3	15.1	0.9	2.5	0.3	4
E.323	-19.4	0.8	13.8	0.3	2.1	0.1	4	-19.1	0.3	14.8	0.5	2.4	0.2	5
E.160	-16.7	0.5	14.2	1.2	2.3	0.4	2	-17.0	0.5	14.9	2.0	2.5	0.6	6
E.115	na	na	na	na	na	na	na	-18.5	0.5	14.4	0.6	2.3	0.2	4
E.GF1	na	na	na	na	na	na	na	-17.4	0.0	14.1	na	2.2	na	1
E.GF2	na	na	na	na	na	na	na	-20.2	0.0	14.2	na	2.2	na	1

Table 18 continued.

Station code	SDF + SSDF feeding guild							P/S feeding guild						
	δ^{13}C	± SE	δ^{15}N	± SE	TL	± SE	n	δ^{13}C	± SE	δ^{15}N	± SE	TL	± SE	n
Shelf (< 200 m)														
W.420	na	na	na	na	na	na	na	-20.1	0.4	12.4	0.4	3.1	0.1	6
W.438	-20.2	0.2	8.8	0.5	2.0	0.1	5	-20.8	0.7	12.2	1.1	3.1	0.3	4
C.314A	-19.8	na	9.5	na	2.3	na	1	-19.0	0.3	16.1	1.0	4.2	0.3	2
C.314B	-18.8	na	9.0	na	2.1	na	1	-18.9	0.5	16.2	0.8	4.2	0.2	4
C.312A	-17.7	na	8.3	na	1.9	na	1	-19.5	0.2	15.1	1.0	3.6	0.6	2
C.312B	-18.1	na	9.3	na	2.2	na	1	-18.7	0.6	13.9	1.3	3.9	0.2	5
C.310F	-18.5	na	6.3	na	1.3	na	1	-19.5	0.5	16.4	1.1	4.3	0.3	3
C.331	-15.0	na	6.8	na	1.5	na	1	-14.8	1.3	13.4	3.3	3.4	1.0	2
C.332	-14.7	na	6.6	na	1.4	na	1	-16.6	1.0	15.7	1.5	4.1	0.4	2
E.150	na	na	na	na	na	na	na	-15.4	0.6	13.8	1.8	3.5	0.5	4
Slope (≥ 200 m)														
W.437	na	na	na	na	na	na	na	na	na	na	na	na	na	na
W.407	-19.6	0.4	14.1	3.1	2.2	0.9	3	-22.3	0.0	11.9	na	1.6	na	1
C.310M	-20.9	na	8.5	na	0.6	na	1	na	na	na	na	na	na	na
C.307	na	na	na	na	na	na	na	-19.8	0.0	12.9	na	1.9	na	1
C.304	-20.3	0.6	9.0	1.6	0.7	0.5	3	-18.4	0.2	14.0	1.1	2.2	0.3	2
E.301	-18.6	na	12.0	na	1.6	na	1	-17.5	0.6	14.9	0.9	2.5	0.3	4
E.323	-18.9	0.1	13.6	0.1	2.1	0.0	2	-16.5	0.7	15.7	1.2	2.7	0.3	3
E.160	na	na	na	na	na	na	na	-17.6	0.8	15.7	0.7	2.7	0.2	3
E.115	-18.3	0.2	13.7	1.0	2.1	0.3	3	-18.1	0.5	13.9	0.5	2.2	0.2	6
E.GF1	na	na	na	na	na	na	na	-17.6	0.3	15.2	1.3	2.5	0.4	4
E.GF2	-20.4	na	12.6	na	1.8	na	1	-19.6	0.3	14.7	0.2	2.4	0.1	7

SF: suspension feeder; SF/SDF: facultative suspension feeder/deposit feeder; SDF: surface deposit feeder; SSDF: subsurface deposit feeder; P/S: predator-scavenger. For data analysis, SDF and SSDF guilds were merged (SDF + SSDF). n: number of taxa analyzed. na: data not available. δ^{13}C and δ^{15}N values of each species/taxon are given in Appendix 4.

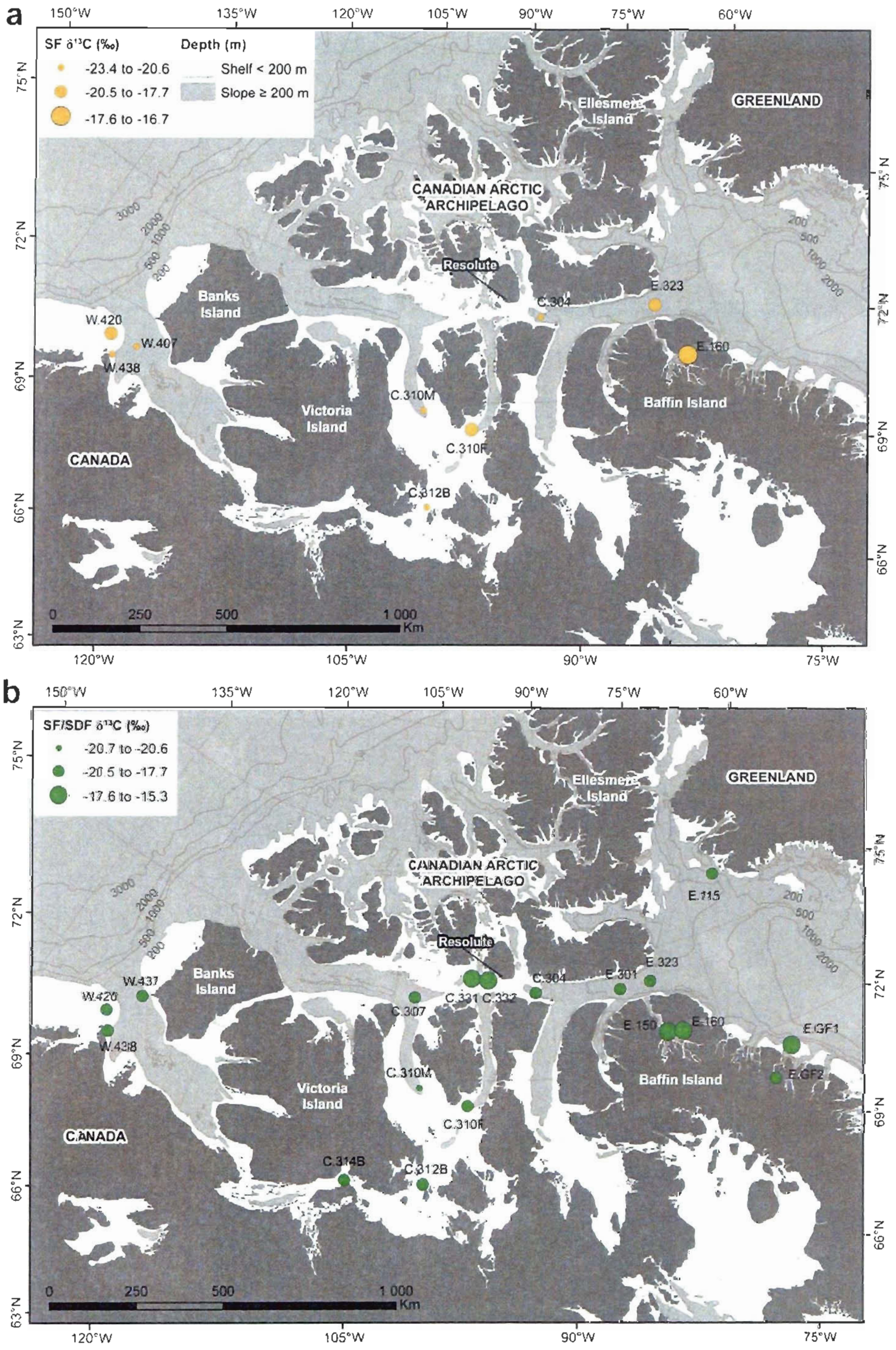

Figure 31. Spatial variations in $\delta^{13}C$ for the benthic feeding guilds (**a**) SF: orange circles (n = 9 stations), (**b**) SF/SDF: green circles (n = 18 stations), (**c**) SDF + SSDF: black circles (n = 13 stations), (**d**) P/S: red circles (n= 17 stations). Break values were determined according to $\delta^{13}C$ data range of all benthic feeding guilds grouped together, but lower and upper bounds (min and max values) are specific to each feeding guild.

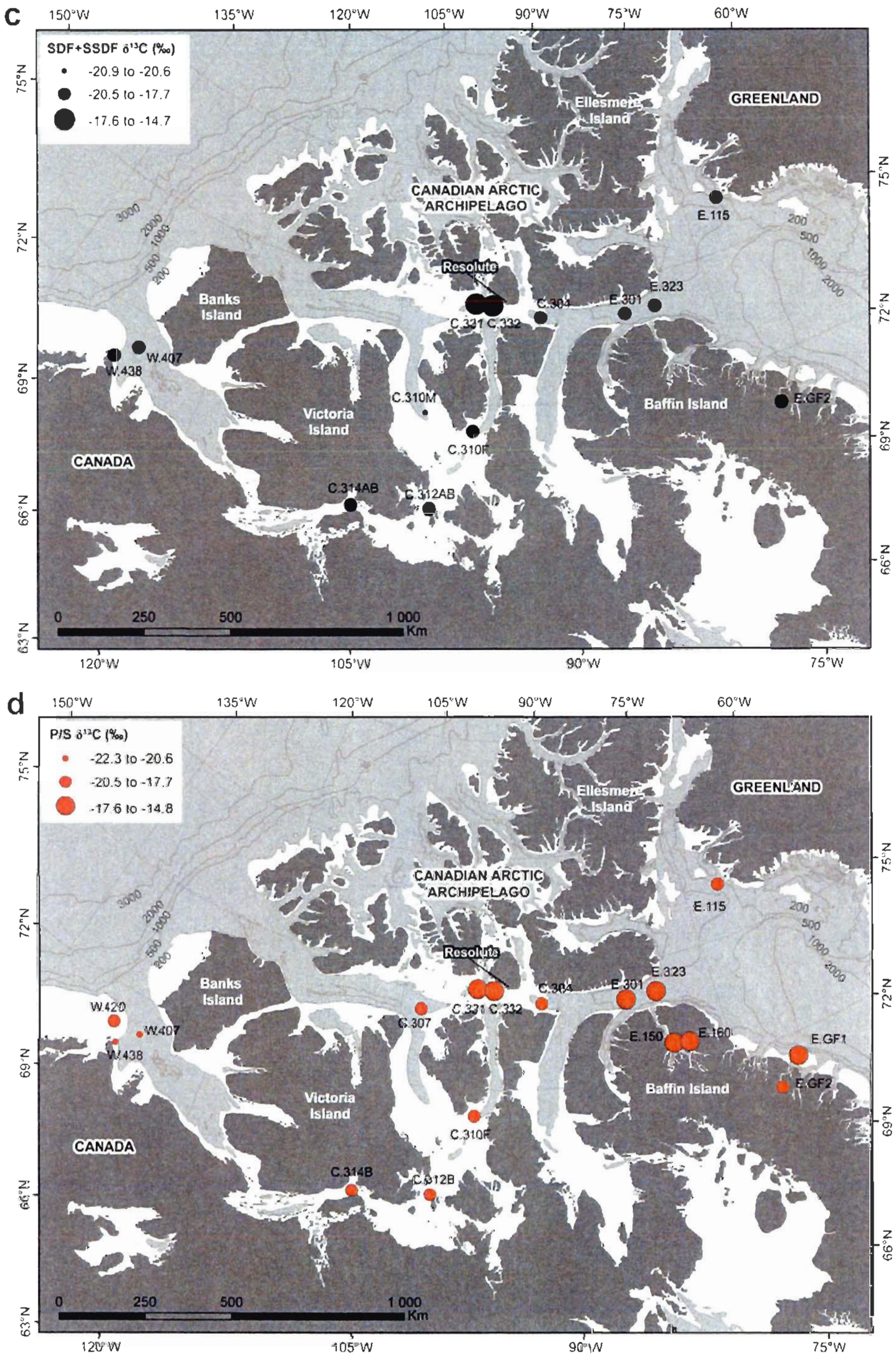

Figure 31 continued. (**c**) SDF + SSDF: black circles (n = 13 stations), (**d**) P/S: red circles (n= 17 stations).

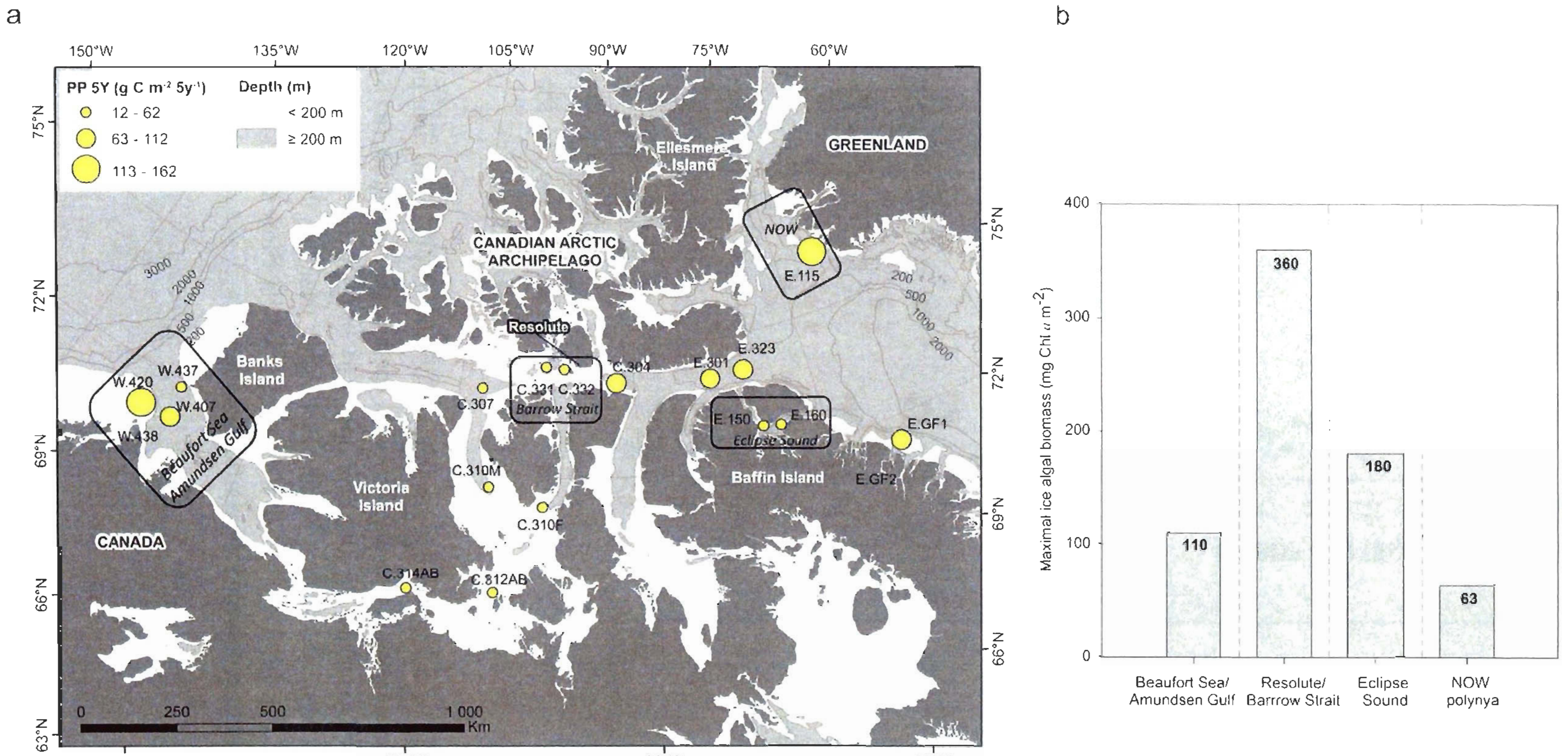

Figure 32. (**a**) Spatial variation in satellite-derived phytoplankton production integrated over a period of 5 years before sampling (PP 5Y; yellow circles; g C m^{-2} $5y^{-1}$; data not available at stations W.438 and E.GF2; geographical pattern of PP 1Y not shown but similar). (**b**) Maximal ice algal chlorophyll *a* biomasses recorded in previous studies in the four regions delimited by the boxes in (**a**) (see text for details).

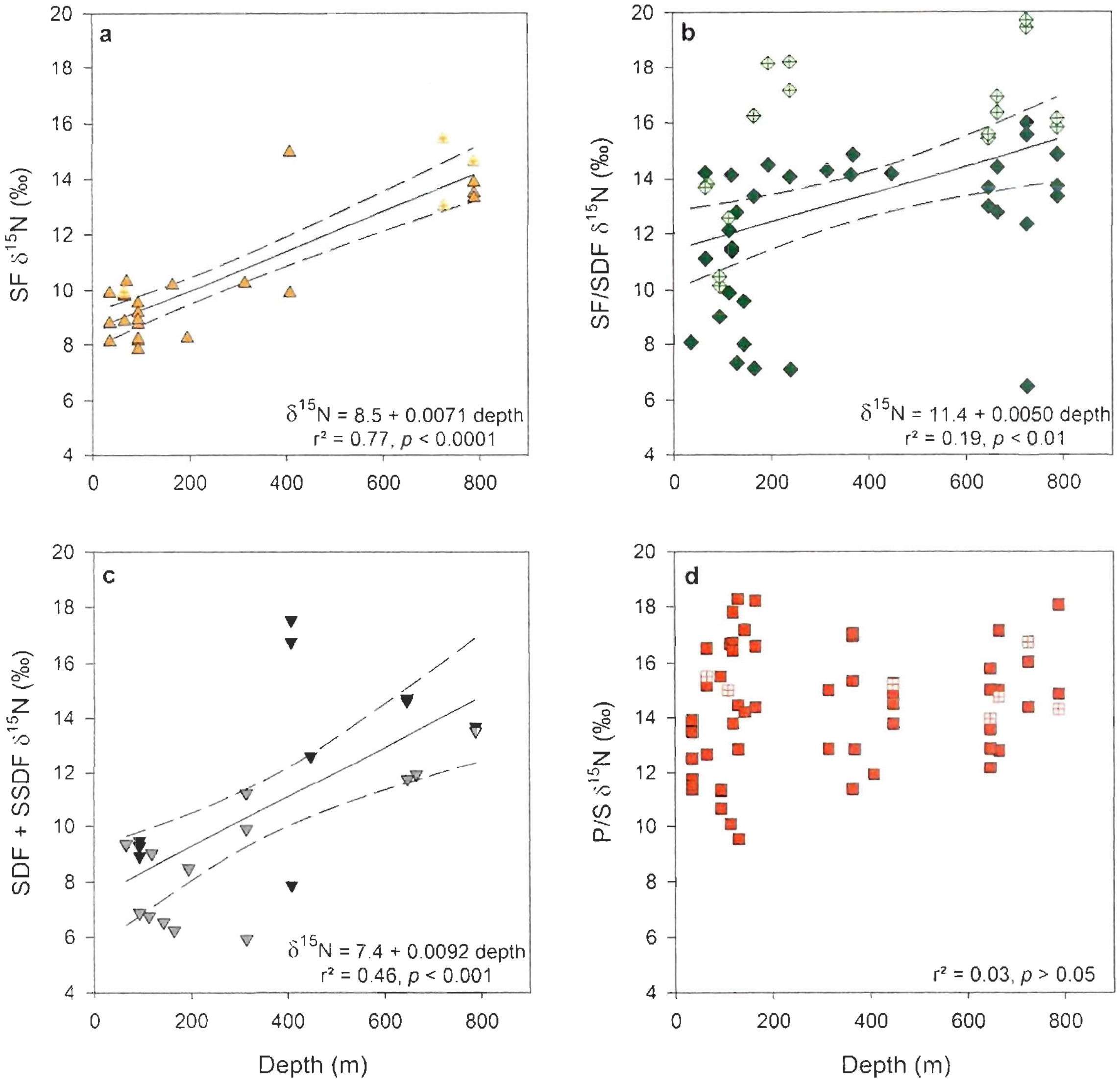

Figure 33. Linear regressions of δ^{15}N of four benthic feeding guilds with depth. Each data point represents the mean δ^{15}N value of one taxon at one station for its specific feeding guild. (**a**) SF (n = 25), crossed symbols show the bryozoans *Alcyonidium* spp.; (**b**) SF/SDF (n = 49), crossed symbols show the bivalves *Astarte* spp.; (**c**) SDF + SSDF: SDF: gray triangles down (n = 14), SSDF: black triangles down (n = 10); (**d**) P/S (n = 61), crossed symbols show the polychaete *Aglaophamus malmgreni*. Dashed lines represent 95% confidence intervals.

Food-web structure

Food-web structure was compared between shelf and slope stations; food-web baseline value ($\delta^{15}N_{\text{selected SF}}$) on the shelf was 8.6 ± 1.1 ‰ (n = 3 SF taxa) and on the slope 13.4 ± 2.0 ‰ (n = 5 SF taxa). The range of trophic level values (TL) differed between the two depth categories: shelf stations ranged from TL 1.3 to TL 4.8, while slope stations ranged from TL 0 to 3.9 (Figure 34). At slope stations, some primary consumers ended up with TL < 1, 1 being the TL value of primary producers. The latter were mostly the brittle stars *Ophiura robusta* (SF/SDF) and *Ophiocten sericeum* (SDF), the mollusk Chaetodermatida (SSDF) and the bryozoan Schizoporellidae (SF). Mean TLs of primary consumers (SF, SF/SDF and SDF + SSDF) were not significantly different between shelf and slope stations (*t*-tests, $p > 0.05$), but mean TL of secondary consumers (P/S) was significantly higher at shelf than at slope stations (*t*-test, $p < 0.05$). TL variances of SF and SDF + SSDF guilds were significantly lower at shelf stations than at slope stations (*F*-test, $p < 0.05$), TL variance of SF/SDF was not significantly different between shelf and slope stations (*F*-test, $p > 0.05$), and TL variances of P/S were significantly higher at shelf than at slope stations (*F*-test, $p < 0.05$) (Figure 34).

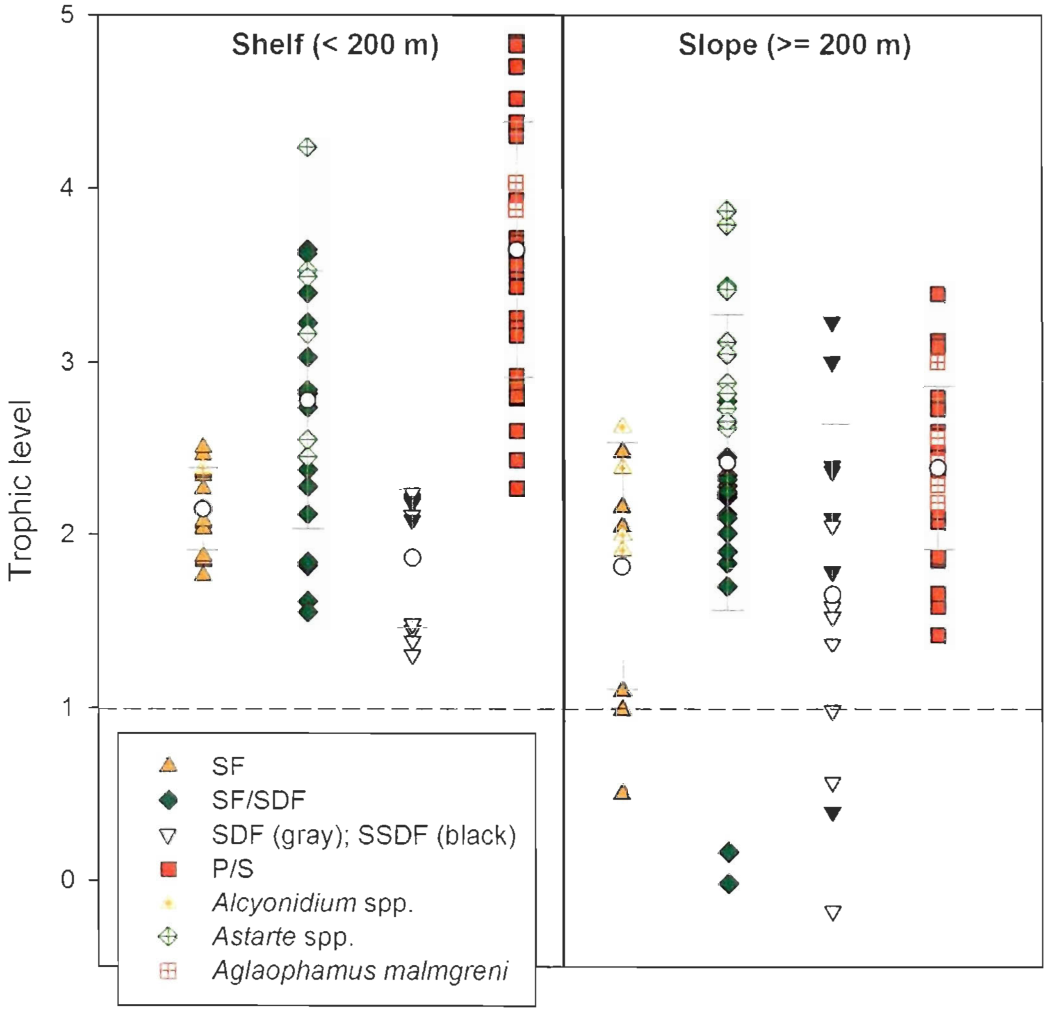

Figure 34. Trophic level (TL) structure at two different depth categories (shelf and slope) for four benthic feeding guilds (SF, SF/SDF, SDF + SSDF and P/S) when considering the food-web baseline as a selection of SF taxa for each depth category (see text for details). Each data point represents the mean TL of one taxon at one depth category for its specific feeding guild. For each feeding guild, mean TL ± standard deviation is shown (filled white circles and gray lines). Dashed black line at TL 1 symbolizes TL of primary producers.

DISCUSSION

The $\delta^{13}C$ variability in food sources and consumers was mostly governed by marine productivity regimes, while $\delta^{15}N$ variability mostly reflected a depth gradient, supporting our hypothesis. Our results shed light on the diverse biological and biochemical processes associated with the different spatial variability patterns exhibited by the food sources and the benthic consumers. We suggest that the high benthic consumer $\delta^{13}C$ values were largely driven by an uncharacterised food source at the time of sampling, i.e., sea-ice algae. The $\delta^{13}C$ spatial variability in benthic consumers did not correlate with spatial patterns of primary productivity in open waters but coincided with the known spatial variability in maximal ice algal biomass. The spatial $\delta^{15}N$ patterns of Bot-POM and benthic consumers revealed that primary consumers at slope stations had access to degraded POM and that secondary consumers likely increased their level of omnivory with depth due to scarcity of prey. These results increase our understanding of constraints of primary carbon sources and level of food degradation for shelf and slope benthic communities in a changing Arctic where the magnitude and composition of food supply have a significant role in shaping benthic communities.

Organic matter sources

SCM-POM showed high seasonal and spatial $\delta^{13}C$ and $\delta^{15}N$ variability, driven mainly by the biomass of large phytoplankton cells (≥ 5 µm) at the time of sampling. In marine systems, enhanced phytoplankton growth, particularly of large cells, often leads to increasing $\delta^{13}C$ and $\delta^{15}N$ values due in part to differential uptake of carbon dioxide (CO_2) vs. bicarbonate (HCO_3^-) (Descolas-Gros & Fontugne 1990; Rau *et al.* 1990; Burkhardt *et al.* 1999) and due to increasing nitrate demand (Wada & Hattori 1978; Needoba *et al.* 2003). As POM produced in surface waters settles below the euphotic zone (Bot-POM), biological and biochemical processes may alter its stable isotope composition. In particular, the high Bot-POM $\delta^{15}N$ values measured at slope stations relative to shelf stations in the present study support conclusions made previously in several marine systems about the greater degradation state of POM reaching deep stations (Altabet 1988; Mintenbeck *et al.*

2007). This pattern is mainly attributed to nitrogen isotopic fractionation during bacterial remineralization and zooplankton scavenging that results in the preferential release of ^{14}N and a ^{15}N enrichment of the residual POM (Macko & Estep 1984; Checkley & Miller 1989). In contrast, Bot-POM $\delta^{13}C$ values did not increase with depth, but were somewhat reduced at deep stations. Fecal pellets of zooplankton are depleted in ^{13}C relatively to the food ingested (Tamelander *et al.* 2006b) and bacterial degradation may cause depletion of ^{13}C in the remnant substrate (Macko & Estep 1984). Overall, the more pronounced $\delta^{15}N$ variability over $\delta^{13}C$ variability in Bot-POM with depth observed here corresponds to the preferential degradation of nitrogen over carbon by hydrolytic enzymatic activity of bacteria (Smith *et al.* 1992). The stable isotope composition of Bot-POM can also be a function of the particle size as smaller suspended particles are subject to higher level of degradation because they tend to stay longer in the water column than larger particles (Altabet 1988; Mintenbeck *et al.* 2007). In this study, we did not investigate stable isotope composition of size-fractionated Bot-POM, but this could provide further insight about the relative importance of particle size and microbial degradation in causing increasing Bot-POM $\delta^{15}N$ values with depth across the study area.

We found indications suggesting that both surface sediment $\delta^{15}N$ and $\delta^{13}C$ values reflected long-term spatial variability in pelagic PP regimes in surface waters. The large $\delta^{15}N$ range (5.8 to 11.1 ‰) exhibited by sediments with a predominantly marine POM origin likely mirrored differences in surface water nitrate conditions under which phytoplankton-derived POM was produced. Because of isotopic fractionation, phytoplankton $\delta^{15}N$ values increase under low nitrate conditions (Altabet & François 1994). The variability in the phytoplankton $\delta^{15}N$ is transmitted to the sediment when euphotic POM sinks: high sediment $\delta^{15}N$ values generally indicate nitrate-depleted surface waters, whereas low and constant sediment $\delta^{15}N$ values indicate nitrate replenishment and productive areas, e.g., through upwelling (Altabet & François 1994; Schubert & Calvert 2001). For instance, the significant negative correlations found between sediment $\delta^{15}N$ values and integrated PP 1Y and PP 5Y illustrated that, at stations with low surface sediment $\delta^{15}N$ values, constant and high nitrate replenishment likely led to high annual PP levels. Diagenetic processes did not appear to affect sediment $\delta^{15}N$ variability in the present study since there was no significant correlation between sediment $\delta^{15}N$ values and surface sediment nitrogen content (%) (Granger *et al.* 2011). The fact that post-production processes influenced the Bot-POM $\delta^{15}N$ values differently across depth, as we showed above, did not seem to strongly affect the sediment $\delta^{15}N$ signature. It is thus highly probable that the sediment $\delta^{15}N$ signature reflected a nitrogen pool derived from large sinking phytoplankton cells as opposed to nitrogen derived from small suspended particles in Bot-POM. The latitudinal ^{13}C enrichment in surface sediments from south to north also indicated that mainly large phytoplankton biomass exhibiting high $\delta^{13}C$ contributed to the marine sediment POM pool in northern stations, corresponding with the productive areas of Lancaster Sound and NOW polynya (Ardyna *et al.* 2011). This geographic gradient coincided also with regional differences in the proportion of marine and terrigenous POM with higher (more marine) sediment $\delta^{13}C$ values measured in the central Canadian Archipelago and in the Eastern Canadian Arctic than in the Western Canadian Arctic, the latter region being highly influenced by the terrestrial inputs from the Mackenzie River (Goni *et al.* 2013). However, since we excluded stations with a strong terrestrial signal from the analysis, this factor less likely influenced the sediment $\delta^{13}C$ variability than the variability in pelagic PP regimes. The significant positive correlation between surface sediment $\delta^{13}C$ and sediment pigments in our study area furthermore indicated the contribution of variable marine POM inputs reaching the seafloor in shaping the spatial variability in surface sediment $\delta^{13}C$.

Benthic faunal assimilation pathways

The $\delta^{13}C$ end-members for the Canadian Arctic benthic food-webs could not be clearly discerned from the three potential food sources analyzed (SCM-POM, Bot-POM and surface sediment) for the over 75 benthic taxa surveyed belonging to four feeding guilds. The primary consumers SF/SDF were enriched in ^{13}C on average by 6.6 ‰ compared with an average of the pelagic-POM (SCM- and Bot-POM) and surface sediment POM values combined. Considering a maximum isotopic enrichment of 2 ‰ per trophic step for $\delta^{13}C$ (Post 2002), direct consumption of pelagic and sedimentary POM was likely not the main carbon assimilation pathways for benthic invertebrates. Although seasonally variable, Ice-POM is on average enriched in ^{13}C by 4-5 ‰ compared to pelagic-POM (Hobson *et al.* 2002; Tamelander *et al.* 2006a; Carroll *et al.* 2014), but across our study area Ice-POM was on average enriched in ^{13}C by 7 ‰ compared to pelagic-POM. Highest ^{13}C enrichments in benthos were observed in the northeastern part of the study area, i.e., in Resolute Passage/Barrow Strait and Eclipse Sound. Across the Canadian Arctic, these two regions exhibit maximal sea-ice algal biomass records (Cross 1982; Cota *et al.* 1991), and the highest concentrations of the sea-ice algal biomarker IP_{25} were measured in Barrow Strait surface sediment and Ice-POM (Belt *et al.* 2010; Belt *et al.* 2013). Thus, the generally higher $\delta^{13}C$ values of benthic consumers over measured food sources, plus the geographical variability in benthic consumer $\delta^{13}C$ values observed among stations in this study, were likely reflecting the spatial variability in sea-ice algae. Ice-POM $\delta^{13}C$ values increase with increasing sea-ice algal biomass (Tremblay *et al.* 2006b; Gradinger 2009; Pineault *et al.* 2013), suggesting that the high benthic organism $\delta^{13}C$ values at Resolute Passage/Barrow Strait and Eclipse Sound mirrored the assimilation of carbon originating from large standing stocks of sea-ice algae. The abundance of large sympagic diatoms primarily accounts for the increasing Ice-POM $\delta^{13}C$ values compared to small flagellates (Pineault *et al.* 2013), and with their high sinking rate (Michel *et al.* 2006; Pineault *et al.* 2013), they contribute largely to the POM pool available for benthos. Similar reliance of Arctic benthic communities on sea-ice algae through tight sympagic-benthic coupling has been reported for the Svalbard Archipelago (Søreide *et al.* 2013).

Our sampling occurred after the seasonal sea-ice algal sedimentation, which occurs on average between May and July across the Canadian Arctic (Michel *et al.* 2002; Michel *et al.* 2006; Juul-Pedersen *et al.* 2008). However, the sea-ice algal signal in benthic consumers can be detected several months after the actual deposition event and one cannot assume that sediment POM at the time of sampling reflects what has been consumed by benthic organisms since the beginning of the growth season. Indeed, a number of Arctic studies showed that sediment $\delta^{13}C$ values do not overlap with those of benthic organisms (e.g., Iken *et al.* 2005; McTigue & Dunton 2013; Søreide *et al.* 2013). The surface sediment POM may represent the bulk POM pool from which benthic taxa, owing to their specific feeding habits, target their preferred POM source(s). Selection of POM particles based on their size, quality, and composition may include selection of ice algal-derived POM and thus lead to the high $\delta^{13}C$ values observed in some benthic consumers. Based on the slow turnover time in Arctic benthic consumer tissues (McMahon et al. 2006, Kaufman et al. 2008, Weems et al. 2012) and on the low benthic organism $\delta^{13}C$ seasonal variability (< 1 ‰) recorded in previous Arctic studies (Dunton *et al.* 1989; Kedra *et al.* 2012; Legezynska *et al.* 2012; Søreide *et al.* 2013; Carroll *et al.* 2014) and in this study, isotopic enrichment from ice algal ingestion should be measurable even months after the sea-ice algal deposition.

Several recent studies in the north-central Bering Sea and the Chukchi Sea proposed that the majority of carbon sources assimilated by benthic organisms passed through the benthic microbial food web, increasing the $\delta^{13}C$ of consumers (Lovvorn *et al.* 2005; Iken *et al.* 2010; McTigue & Dunton 2013). These studies did not include ice algae as a source of ^{13}C enrichment as ice algae were not present at the time of sampling. We suggest here that benthic $\delta^{13}C$ values were not primarily indicative of assimilation of microbial-derived POM but of long-term effects of ice algal deposition and ingestion. In the Svalbard Archipelago, fatty acid profiles revealed on average a low proportion of bacterial fatty acid trophic marker in benthic invertebrates compared to the high proportion of diatom fatty acid trophic marker (Søreide *et al.* 2013). Nonetheless, the benthic microbial food web may have increased the already high $\delta^{13}C$ signature of ice algal-derived POM (Sun *et al.* 2009), ultimately resulting in very high benthic $\delta^{13}C$ values decoupled from pelagic-POM and sediment $\delta^{13}C$ values. Microbial processing alone could not explain the geographical patterns we observed in benthic organism $\delta^{13}C$ values. For example, the two stations located in Eclipse Sound were relatively close to each other (50 km apart) but were positioned in distinct water masses: station E.150 was in the colder-fresher Pacific water mass at 130 m water depth, while station E.160 was in the warmer-saline Atlantic water mass at 726 m water depth (Figure 27, Table 13). We expect the bottom bacterial community to differ between these two locations as bacterial abundance, composition and activity are greatly affected by environmental factors, such as temperature and oxygen (Sander & Kalff 1993). Consequently, the similar benthos $\delta^{13}C$ values measured at these two stations presumably suggested that the isotopic carbon source signature reflected surface primary production (i.e., ice algae) and not benthic microbial food-web processes. However, the $\delta^{15}N$ variability of benthic primary consumers with depth showed an increasing assimilation of ^{15}N enriched POM with depth. Therefore, the $\delta^{13}C$ and $\delta^{15}N$ signatures of the deep benthic primary consumers suggest that they ingested ice algal-derived POM (as seen by high $\delta^{13}C$ values) that was reworked by the pelagic and/or benthic microbial food webs (as seen by high $\delta^{15}N$ values).

Food-web structure

Increasing primary consumer $\delta^{15}N$ values with depth confirmed our choice of using shelf- and slope-specific suspension feeders as food-web baselines instead of generalizing the baseline across the entire depth gradient. We demonstrated that post-production processes (e.g., microbial degradation and zooplankton grazing) along the shelf-slope gradient likely influenced settling POM $\delta^{15}N$ values, as it was also demonstrated in the Antarctic Weddell Sea (Mintenbeck *et al.* 2007). Our approach led to similar mean trophic levels (TL) for primary consumers collected on the shelf and on the slope, thus not affecting the trophic hierarchy and allowing unbiased comparisons. However, the variances around mean TL values for some primary consumer guilds (SF, SDF + SSDF) were lower on the shelf than on the slope, mostly due to some TL values < 1. Low variance should be observed in specialist feeders or in generalist feeders exposed to a uniform food supply (Bearhop *et al.* 2004; Sweeting *et al.* 2005). Increasing scarcity of primary producer-derived POM at deep stations potentially triggered some taxa to feed on other food items than their guild counterparts at shelf stations. Microbial processing can increase (see above) or decrease ^{15}N in POM (Macko & Estep 1984), and foraging on depleted ^{15}N microbial-processed POM or on foraminifera, which can have depleted nitrogen isotope signatures (Iken *et al.* 2001; Iken *et al.* 2005; Nomaki *et al.* 2008), could possibly explain the TL < 1 of some of the primary consumer taxa surveyed in the present study. Among these, the SSDF Chaetodermatida are believed to generally burrow in muddy bottom and feed mostly on foraminiferans (Salvini-Plawen 1981; Shigeno *et al.* 2007). TL values < 1 may also indicate that our average slope baseline was not appropriate for all taxa inhabiting slope stations. Additionally, it could be the result of the constant trophic enrichment factor that we used across the study area and taxa, as 3.4 ‰ is an average estimate of trophic fractionation between TL and any single trophic transfer is likely to range between 2 ‰ and 5 ‰ (Post 2002). The mixture of the two facultative feeding modes of the SF/SDF guild likely obscured the depth effect on their trophic niche and suggests that this guild may have the potential to deal with varying amounts and quality of food supply. We merged SDF and SSDF feeding guilds assuming that they had access to isotopically similar POM in the sediment based on the results of McTigue and Dunton (2013), but in the present study, SSDF generally occupied a higher trophic position relative to SDF. Based on the average TL values for each feeding guild at slope stations, we therefore suggest that SDF had more access to labile settled POM as opposed to the more degraded sedimentary POM accessible to SSDF and the degraded suspended or re-suspended POM accessible for SF, in agreement with other studies carried out in deep-sea systems (Iken *et al.* 2001; Mintenbeck *et al.* 2007; Gontikaki *et al.* 2011).

The secondary consumers (P/S) $\delta^{15}N$ values did not increase with depth as primary consumers did, effectively resulting in a decrease of their trophic levels from shelf to slope ecosystems. We suggest that their consistent $\delta^{15}N$ across depth reflected an increasing level of omnivory with depth. Likewise, Bergmann *et al.* (2009) detected no depth-related change in P/S $\delta^{15}N$ values along a bathymetric gradient at the HAUSGARTEN deep-sea observatory in Fram Strait. True benthic predators are often less common than omnivorous feeders in deep-sea systems because of the scarcity of benthic prey organisms (Iken *et al.* 2005). Benthic predators in shallow-waters may potentially expand their feeding preferences in the deep-sea environment to avoid food limitation, resulting in an increase in omnivorous feeding. It may then become impossible at depth to differentiate deposit feeders from 'assumed predators' solely based on their $\delta^{15}N$ values, as observed at a deep-sea station in the Faroe-Shetland Channel (Gontikaki *et al.* 2011). Information on exact feeding modes of benthic invertebrates is scarce, even more so for deep-sea inhabitants (Bergmann *et al.* 2009), but our investigation of the $\delta^{15}N$ trend and trophic position variability in the P/S guild from shelf to slope environments provided insight into the potential diet change for members of this guild across a depth gradient.

The degraded state of POM ingested by deep primary consumers and the increase in omnivorous feeding expressed by deep secondary consumers are in agreement with the decreasing trends of 'fresh' food availability (i.e., sediment Chl *a*) and megabenthic biomass and density along the depth gradient of the study area (Roy *et al.* 2014).

SUMMARY AND IMPLICATIONS

The enriched isotopic carbon signatures of benthic consumers compared with the pelagic-POM and sediment POM, especially in regions of known high ice algal standing stock, led us to the interpretation that ice algae play a vital role in the benthic food webs across the Canadian Arctic. The low reported stable isotopic turnover measured in benthic invertebrate muscle tissues (McMahon et al. 2006, Kaufman et al. 2008, Weems et al. 2012) and the low benthic organism $\delta^{13}C$ seasonal variability recorded in previous Arctic studies (Dunton *et al.* 1989; Kedra *et al.* 2012; Legezynska *et al.* 2012; Søreide *et al.* 2013; Carroll *et al.* 2014) allowed us to track this ice algal signal, even though samples were taken after the sea-ice algal deposition. We showed that spatial variability in carbon stable isotopes could be a valuable tool to trace the flow of ice-derived POM assimilated by benthic organisms, especially in areas of recurrent high ice algal standing stock because of the positive relation between ice algal standing stock and Ice-POM $\delta^{13}C$ values (Tremblay *et al.* 2006b; Gradinger 2009; Pineault *et al.* 2013). This is the first study showing that the spatial variability in ice algal standing stock could be potentially tracked in benthic consumer tissues by the use of carbon stable isotope composition. Further investigations, using fatty acid profiles and compound-specific carbon stable isotope composition of individual fatty acids (Wang *et al.* 2014) and/or using the sea-ice algal biomarker IP_{25} (Brown & Belt 2012) are needed to complement the present study and to confirm the importance of ice algal-derived POM in the overall diet of the Canadian Arctic benthic food webs.

Our analyses also highlighted the importance of exploring the environmental drivers and the temporal scale of variability in pelagic-POM stable isotope compositions before using this potential food source as a food-web baseline for benthic communities, especially in a study area that covers various marine productivity and depth regimes, like the Canadian Arctic. Our results showed that seasonal variability in both SCM-POM and Bot-POM was too high to consider them as good reference baselines for benthic food webs that integrate over longer time scales. We also stressed the importance of using a depth-stratified approach to ensure valid comparisons between shelf and slope benthic food-web structures as benthic slope organisms assimilated POM altered by a number of post-production degradation processes.

Our conclusions indicated that seasonally earlier sea-ice retreat and the parallel decline of sea-ice algal standing stock expected from climate changes (Bluhm & Gradinger 2008) will likely have an impact on the Canadian Arctic benthic communities. The importance of this impact to benthic communities is difficult to predict, but it is conceivable that, at least over the short-term, benthic communities may sustain on sedimentary refractory POM and/or on settling phytoplankton-derived POM. However, if climate changes were to induce a decrease in the strength of the pelagic-benthic coupling (e.g., with increasing zooplankton grazing), current hotspots of benthic biomass will most likely decline over the long-term, with more drastic impacts expected for slope benthic ecosystems than for shelf benthic ecosystems. We propose therefore that this study may serve as a reference for future studies evaluating how the carbon and nitrogen stable isotope compositions of benthic organisms follow naturally and anthropogenic induced ecosystem changes across the Canadian Arctic.

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Appendix 4.

Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) of benthic species/taxon collected in 2011 across the Canadian Arctic. Trophic level (TL) based on selected suspension feeder taxa (*) for baseline calculations (see text for details). Stations are ordered by depth categories (shelf and slope) and by geographical regions (W: west, C: center, E: east). SF: suspension feeder; SF/SDF: facultative suspension feeder/deposit feeder; SDF: surface deposit feeder; SSDF: subsurface deposit feeder; P/S: predator-scavenger. References (Ref) for feeding mode assignment. For data analysis, SDF and SSDF guilds were merged (SDF + SSDF). n: number of individuals analyzed.

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	$\delta^{13}C$	± SD	$\delta^{15}N$	± SD	n	TL
Shelf (< 200 m)										
W.420	SF	[1]	Bivalvia	*Ciliatocardium ciliatum ciliatum*	-20.2		8.1		1	1.8
	SF	[1,2]	Bivalvia	*Hiatella arctica*	-19.7	0.8	9.9	0.5	3	2.4
	SF	[1]	Bivalvia	*Musculus discors*	-20.4	0.1	8.8	0.2	2	2.0
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-18.7	0.3	8.1	1.1	3	1.8
	P/S	[4,5]	Arthropoda	*Anonyx nugax*	-19.9		13.9		1	3.6
	P/S	[5]	Arthropoda	*Eualus gaimardii gaimardii*	-20.2	0.0	13.5	1.2	2	3.4
	P/S	[4]	Arthropoda	*Rhachotropis aculeata*	-21.5		11.8		1	2.9
	P/S	[6]	Polychaeta	*Harmothoe extenuata*	-19.3	0.2	11.5	0.4	2	2.9
	P/S	[6]	Polychaeta	*Nereis zonata*	-20.3		11.4		1	2.8
	P/S	[6]	Polychaeta	*Nothria conchylega*	-19.0	0.0	12.6	1.0	2	3.2
W.438	SF	[7]	Arthropoda	*Ampelisca macrocephala* *	-22.0	0.3	8.1	0.6	3	1.9
	SF	[1]	Arthropoda	*Arctolembos arcticus*	-22.7		8.7		1	2.0
	SF	[4,8]	Arthropoda	*Haploops laevis* *	-22.8	0.3	7.8	0.1	3	1.8
	SF	[1]	Bivalvia	*Ciliatocardium ciliatum ciliatum*	-20.9	0.1	8.9	0.1	3	2.1
	SF	[9]	Bivalvia	*Liocyma fluctuosa*	-20.9		8.2		1	1.9
	SF	[1]	Echinodermata	*Amphiura sundevalli*	-20.1		9.2		1	2.2
	SF	[10]	Hydrozoa	Sertulariidae	-24.1		9.5		1	2.3
	SF/SDF	[11]	Bivalvia	*Astarte borealis*	-19.8		10.2		1	2.4
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-20.4		10.5		1	2.5
	SF/SDF	[12]	Bivalvia	*Macoma calcarea*	-19.9	0.4	9.0	0.3	2	2.1
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-19.7	0.4	6.9	2.4	3	1.5
	SDF	[2]	Echinodermata	*Stegophiura nodosa*	-19.7	0.3	9.3	0.3	3	2.2
	SSDF	[13,14]	Bivalvia	*Ennucula tenuis*	-20.9	0.2	8.9	0.3	3	2.1

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	$\delta^{13}C$	± SD	$\delta^{15}N$	± SD	n	TL
W.438	SSDF	[14]	Bivalvia	*Nuculana pernula*	-20.3	0.5	9.5	0.4	3	2.2
	SSDF	[15,16]	Bivalvia	*Yoldia hyperborea*	-20.5	0.3	9.3	0.4	3	2.2
	P/S	[5]	Arthropoda	*Sabinea septemcarinata*	-19.1		15.5		1	4.0
	P/S	[17]	Arthropoda	*Saduria sabini*	-20.9		11.4		1	2.8
	P/S	[17]	Arthropoda	*Synidotea bicuspida*	-22.4	0.1	11.3	0.3	3	2.8
	P/S	[6]	Polychaeta	*Bylgides promamme*	-20.8		10.7		1	2.6
C.314A	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-19.8	0.1	9.5	0.2	2	2.3
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-19.3		15.0		1	3.9
	P/S	[6]	Polychaeta	*Nephtys incisa*	-18.8		17.1		1	4.5
C.314B	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-20.7	0.2	11.4	0.2	3	2.8
	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-20.8	0.2	11.5	0.4	3	2.8
	SF/SDF	[6,9,16]	Polychaeta	*Spio* sp.	-19.7	0.1	14.2	0.6	2	3.6
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-18.8	1.3	9.0	0.3	3	2.1
	P/S	[5]	Arthropoda	*Sabinea septemcarinata*	-18.7		16.7		1	4.4
	P/S	[6]	Polychaeta	*Nephtys incisa*	-18.2	0.4	17.8	0.9	3	4.7
	P/S	[6]	Polychaeta	*Nephtys longosetosa*	-18.3		16.5		1	4.3
	P/S	[6]	Polychaeta	*Scoletoma fragilis*	-20.4	0.4	13.8	0.6	3	3.5
C.312A	SF	[5]	Arthropoda	*Arcturus baffini tuberosus*	-21.9	0.1	9.3	0.5	3	2.2
	SF	[20]	Bryozoa	*Alcyonidium gelatinosum anderssoni* (sp.A)	-22.5	0.8	9.8	0.2	2	2.3
	SF	[10]	Hydrozoa	Hydrozoa A	-22.1		9.3		1	2.2
	SF	[1]	Echinodermata	*Ophiopus arcticus*	-16.8	0.3	10.3	0.1	3	2.5
	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-20.8		13.8		1	3.5
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-20.7	0.7	14.4	0.6	3	3.7
	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-21.9	0.5	11.5	0.7	3	2.8
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-17.9	1.8	13.6	0.4	3	3.5
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-17.7	0.4	8.3	1.1	3	1.9
	P/S	[4,5]	Arthropoda	*Anonyx nugax*	-19.7	0.7	16.0	0.9	3	4.2
	P/S	[6]	Polychaeta	*Eunoe nodosa*	-19.2	0.8	11.9	0.9	2	3.0
C.312B	SF	[5]	Arthropoda	*Arcturus baffini tuberosus*	-22.0	0.4	8.8	0.6	3	2.1
	SF	[20]	Bryozoa	*Alcyonidium gelatinosum anderssoni* (sp.A)*	-22.5	0.7	9.9	0.6	2	2.4
	SF	[10]	Hydrozoa	Hydrozoa A	-21.2		9.8		1	2.4
	SF	[10]	Hydrozoa	Sertulariidae	-21.6		9.8		1	2.3

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	$\delta^{13}C$	± SD	$\delta^{15}N$	± SD	n	TL
C.312B	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-20.4	0.3	13.7	1.0	3	3.5
	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-20.8	0.4	11.1	0.1	3	2.7
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-18.3	1.6	14.2	0.2	3	3.6
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-18.1	0.9	9.3	0.9	3	2.2
	P/S	[4,5]	Arthropoda	*Anonyx nugax*	-18.9	0.4	16.5	0.7	2	4.3
	P/S	[5]	Arthropoda	*Eualus gaimardii gaimardii*	-20.4		15.2		1	3.9
	P/S	[5]	Arthropoda	*Sabinea septemcarinata*	-17.6	0.1	15.5	1.3	2	4.0
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-17.0	0.7	15.5	0.9	3	4.0
	P/S	[6]	Polychaeta	*Eunoe nodosa*	-19.3	0.5	12.7	0.6	3	3.2
C.310F	SF	[1]	Echinodermata	*Ophiopus arcticus*	-18.9	0.7	10.2	0.1	3	2.5
	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-20.2	1.6	16.2	0.8	3	4.2
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-19.2	0.5	13.4	0.2	3	3.4
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-19.1	0.7	7.1	1.1	3	1.6
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-18.5	0.0	6.3	0.7	2	1.3
	P/S	[4,5]	Arthropoda	*Anonyx nugax*	-20.4	0.2	16.6	1.8	3	4.3
	P/S	[5]	Arthropoda	*Sabinea septemcarinata*	-18.7	0.3	18.2	0.5	3	4.8
	P/S	[6]	Polychaeta	*Eunoe nodosa*	-19.3		14.4		1	3.7
C.331	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-18.8	0.3	12.6	1.9	3	3.2
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-15.8	0.1	12.1	0.3	3	3.0
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-14.3		9.9	0.2	1	2.4
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-15.0		6.8		1	1.5
	P/S	[3]	Echinodermata	*Ophiura sarsii*	-13.5		10.1		1	2.4
	P/S	[6]	Polychaeta	*Nephtys incisa*	-16.1		16.7		1	4.4
C.332	SF/SDF	[12]	Bivalvia	*Macoma calcarea*	-17.9	0.4	9.6	0.3	3	2.3
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-15.6	0.4	8.0	0.6	3	1.8
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-14.7	1.0	6.6	1.2	3	1.4
	P/S	[6]	Polychaeta	*Nephtys incisa*	-17.6		17.2		1	4.5
	P/S	[6]	Polychaeta	*Nephtys longosetosa*	-15.6	0.2	14.2	0.4	2	3.6
E.150	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-14.9	0.7	12.8	1.0	3	3.2
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-15.6	0.6	7.3	0.5	3	1.6
	P/S	[5]	Arthropoda	*Lebbeus polaris*	-16.8	0.3	14.5	0.4	3	3.7
	P/S	[5]	Arthropoda	*Sabinea septemcarinata*	-16.1		12.9		1	3.3

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	δ^{13}C	± SD	δ^{15}N	± SD	n	TL
E.150	P/S	[3]	Echinodermata	*Ophiura sarsii*	-15.1	0.9	9.5	0.2	3	2.3
	P/S	[6]	Polychaeta	*Nephtys incisa*	-13.8		18.3		1	4.8
Slope (≥ 200 m)										
W.437	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-18.5		18.2		1	3.4
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-21.2	0.3	17.1	0.6	3	3.1
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-20.5	1.1	14.1	0.4	3	2.2
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-19.8	1.0	7.1	1.7	2	0.2
W.407	SF	[20]	Bryozoa	*Eucratea loricata*	-22.2		9.9		1	1.0
	SF	[6]	Polychaeta	*Jasmineira* sp.	-21.2	0.4	15.0	0.6	3	2.5
	SSDF	[1]	Arthropoda	*Calathura brachiata*	-20.3		17.5		1	3.2
	SSDF	[21]	Mollusca	Chaetodermatida	-19.0		7.9		1	0.4
	SSDF	[6]	Polychaeta	*Maldane* sp.	-19.5		16.8		1	3.0
	P/S	[6]	Polychaeta	Phyllodocidae	-22.3		11.9		1	1.6
C.310M	SF	[20]	Bryozoa	Schizoporellidae	-23.4		8.2		1	0.5
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-21.3	0.2	18.2	0.1	3	3.4
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-20.1	0.1	14.5	0.3	2	2.3
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-20.9	0.3	8.5	1.0	3	0.6
C.307	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-18.1	0.8	14.9	0.8	3	2.4
	P/S	[3]	Echinodermata	*Ophioscolex glacialis*	-19.8	0.1	12.9	0.0	2	1.9
C.304	SF	[7]	Arthropoda	*Ampelisca eschrichtii* *	-21.4		10.3		1	1.1
	SF/SDF	[6,9,16]	Polychaeta	*Spio* sp.	-18.9		14.3		1	2.3
	SDF	[22]	Bivalvia	*Portlandia* sp.	-20.7		9.9		1	1.0
	SDF	[8]	Echinodermata	*Ophiocten sericeum*	-19.2	0.5	6.0	0.9	2	-0.2
	SDF	[6]	Polychaeta	Terebellinae	-21.0	0.4	11.2	0.9	3	1.4
	P/S	[8,23]	Echinodermata	*Hymenaster pellucidus*	-18.2		12.9		1	1.9
	P/S	[6]	Polychaeta	Lumbrineridae	-18.6		15.0		1	2.5
E.301	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-17.3	0.3	16.3	1.0	3	2.9
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-18.3		16.9		1	3.0
	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-18.1	1.1	14.4	0.1	2	2.3
	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-18.5		12.8		1	1.8

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	$\delta^{13}C$	± SD	$\delta^{15}N$	± SD	n	TL
E.301	SDF	[6]	Polychaeta	*Amphicteis gunneri*	-18.6		12.0		1	1.6
	P/S	[5]	Arthropoda	*Lebbeus polaris*	-18.7		15.0		1	2.5
	P/S	[3]	Echinodermata	*Ophiopleura borealis*	-16.9		12.8		1	1.8
	P/S	[23]	Echinodermata	*Psilaster andromeda*	-16.2		17.1		1	3.1
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-18.1	0.4	14.8	0.6	3	2.4
E.323	SF	[1]	Arthropoda	*Scalpellum* sp.	-20.6		13.5		1	2.0
	SF	[20]	Bryozoa	*Alcyonidium* sp.E (ramified)*	-17.8		13.3		1	2.0
	SF	[20]	Bryozoa	*Alcyonidium gelatinosum anderssoni* (sp.A)*	-18.3	0.8	14.7	1.9	4	2.4
	SF	[10]	Hydrozoa	Lafoeidae	-21.0		13.9		1	2.2
	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-18.3	0.1	16.1	0.1	3	2.8
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-18.5	0.1	15.8	0.4	3	2.7
	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-19.1	0.5	13.7	0.2	3	2.1
	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-20.1	0.3	13.4	0.2	3	2.0
	SF/SDF	[1]	Bivalvia	*Cuspidaria glacialis*	-19.3	0.4	14.9	0.2	3	2.4
	SDF	[6]	Polychaeta	*Melinna cristata*	-18.8		13.5		1	2.1
	SSDF	[6]	Polychaeta	*Asychis biceps*	-18.9	0.3	13.7	1.3	3	2.1
	P/S	[3]	Echinodermata	*Ophiopleura borealis*	-15.4		14.9		1	2.4
	P/S	[23]	Echinodermata	*Psilaster andromeda*	-16.2	0.2	18.1	1.2	3	3.4
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-17.9	0.0	14.3	0.8	3	2.3
E.160	SF	[20]	Bryozoa	*Alcyonidium cf gelatinosum anderssoni* (sp.B)*	-17.2		15.5		1	2.6
	SF	[20]	Bryozoa	*Alcyonidium gelatinosum anderssoni* (sp.A)*	-16.2		13.0		1	1.9
	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-16.2	0.9	19.7	0.3	3	3.9
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-14.9	0.5	19.4	0.8	3	3.8
	SF/SDF	[18,19]	Bivalvia	*Bathyarca glacialis*	-18.1	0.5	16.0	0.7	2	2.8
	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-18.2	0.1	15.6	0.2	3	2.6
	SF/SDF	[3]	Echinodermata	*Ophiura robusta*	-18.2	0.7	6.5	0.1	3	0.0
	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-16.6	1.0	12.3	1.5	3	1.7
	P/S	[15]	Arthropoda	*Hymenodora glacialis*	-19.1	0.2	14.4	0.4	3	2.3
	P/S	[5]	Arthropoda	*Lebbeus polaris*	-17.4		16.0		1	2.8
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-16.3	0.7	16.7	0.3	3	3.0
E.115	SF/SDF	[11,19]	Bivalvia	*Astarte crenata*	-17.5	0.5	15.4	0.7	3	2.6
	SF/SDF	[11]	Bivalvia	*Astarte montagui*	-18.5	0.4	15.6	0.3	3	2.7
	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-19.9		13.0		1	1.9

Station code	Feeding guild	Ref	Taxonomic group	Species or Taxon	$\delta^{13}C$	± SD	$\delta^{15}N$	± SD	n	TL
E.115	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-18.1	1.1	13.7	0.8	3	2.1
	SDF	[6]	Polychaeta	*Thelepus cincinnatus*	-18.5	0.5	11.8	0.9	3	1.5
	SSDF	[6]	Polychaeta	*Asychis biceps*	-18.3		14.6		1	2.4
	SSDF	[6]	Polychaeta	*Nicomache* sp.	-17.9	0.5	14.7	0.8	2	2.4
	P/S	[3]	Echinodermata	*Ophiopleura borealis*	-16.2	0.9	13.6	0.9	2	2.1
	P/S	[3]	Echinodermata	*Ophiura sarsii*	-17.4	0.1	12.9	1.1	3	1.9
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-17.8	0.4	14.0	0.9	3	2.2
	P/S	[6]	Polychaeta	*Eunoe nodosa*	-18.6		15.0		1	2.5
	P/S	[6]	Polychaeta	*Nothria conchylega*	-20.0		12.2		1	1.7
	P/S	[6]	Polychaeta	*Scoletoma fragilis*	-18.4		15.8		1	2.7
E.GF1	SF/SDF	[3]	Echinodermata	*Ophiacantha bidentata*	-17.4	0.3	14.1	0.7	3	2.2
	P/S	[8]	Arthropoda	*Bythocaris gracilis/payeri*	-18.2	1.0	17.0	0.9	3	3.1
	P/S	[5]	Arthropoda	*Lebbeus polaris*	-18.0	0.4	15.4	1.0	3	2.6
	P/S	[5]	Arthropoda	*Sclerocrangon ferox*	-17.1		17.0		2	3.1
	P/S	[3]	Echinodermata	*Ophiura sarsii*	-17.2	0.7	11.4	1.2	3	1.4
E.GF2	SF/SDF	[18,19]	Bivalvia	*Bathyarca* sp. (< 1.5 cm)	-20.2		14.2		1	2.2
	SSDF	[6]	Polychaeta	Scalibregmatidae	-20.4	0.1	12.6	0.9	2	1.8
	P/S	[5]	Arthropoda	*Eualus gaimardii belcheri*	-19.7		14.8		1	2.4
	P/S	[3]	Echinodermata	*Ophiopleura borealis*	-18.3	0.7	14.9	1.0	3	2.4
	P/S	[3]	Echinodermata	*Ophiura sarsii*	-18.8	0.4	14.6	0.3	3	2.4
	P/S	[6]	Polychaeta	*Aglaophamus malmgreni*	-19.3	0.5	15.2	0.4	2	2.6
	P/S	[6]	Polychaeta	*Bylgides groenlandicus*	-20.0		14.5		1	2.3
	P/S	[6]	Polychaeta	*Nothria conchylega*	-20.9	0.3	13.8	0.5	3	2.1
	P/S	[6]	Polychaeta	*Scoletoma fragilis*	-20.2		15.3		1	2.6

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CONCLUSION GÉNÉRALE

Les trois objectifs globaux de cette thèse étaient : (1) d'en faire une étude de référence en apportant de nouvelles données sur la diversité et la distribution des communautés benthiques de la macrofaune et mégafaune de l'Arctique canadien; (2) de déterminer comment les facteurs environnementaux structurent ces communautés benthiques; et (3) de transférer en partie les résultats aux instances gouvernementales, principalement Pêches et Océans Canada, afin d'enrichir l'état des connaissances des écosystèmes benthiques de l'Arctique canadien et d'appuyer la désignation de ZIEB. Ces trois grands objectifs ont été atteints avec succès. Cette thèse apporte les premières données de référence sur la richesse taxonomique et la distribution des communautés de la mégafaune benthique à l'échelle de l'Arctique canadien (chapitres 1 et 2). Elle apporte également de nombreuses données originales quant aux compositions isotopiques en carbone et en azote d'organismes benthiques à travers l'archipel arctique canadien (chapitre 4). Le rôle de divers facteurs environnementaux intégrant des variabilités spatiales et temporelles à des échelles différentes fut testé dans la majorité des chapitres (chapitres 2, 3 et 4). Les chapitres 1, 2 et 3 de cette thèse étaient développés dans un souci de transfert de connaissances vers Pêches et Océans Canada et ont directement contribué à ma participation à deux consultations scientifiques nationales du secrétariat canadien de consultation scientifique (SCCS) de Pêches et Océans Canada et à l'écriture de deux documents de recherche associés, un publié (Kenchington *et al.* 2011) et un en cours de publication (Cobb *et al.* 2014). Voici les contributions spécifiques qu'apportent mes quatre chapitres.

CONTRIBUTIONS DE L'ÉTUDE

Premier recensement de la diversité de la mégafaune benthique à l'échelle de l'Arctique canadien

Le premier chapitre de cette thèse a, tout d'abord, permis d'établir que l'échantillonnage effectué jusqu'à ce jour à travers l'Arctique canadien pour la mégafaune benthique a permis de recenser une riche diversité taxonomique avec 527 taxa identifiés au plus bas niveau taxonomique possible, dont 430 au niveau de l'espèce. Toutefois, en moyenne près de 50 % des taxa restent à recenser (régionalement entre 34 et 59 % selon les courbes d'accumulation de taxa). Ceci démontre d'une part la grande richesse benthique des fonds marins de l'Arctique canadien, et illustre d'autre part que toutes campagnes d'échantillonnage éventuelles seront capitales pour augmenter le recensement de la diversité marine benthique. Moins d'efforts d'échantillonnage ont été conduits dans le cœur de l'archipel canadien que dans les régions de la mer de Beaufort, le golfe d'Amundsen et le nord de la baie de Baffin, surtout en raison des objectifs des missions des réseaux scientifiques et également en raison de la présence plus forte de glace multiannuelle au cœur de l'archipel. L'archipel recèle pourtant d'endroits très intéressants à étudier d'un point de vue benthique. Entre autres, le chapitre 2 a montré que certains endroits au cœur de l'archipel abritent des communautés mégabenthiques possédant de fortes biomasses et richesses (« *local hotspots* »), notamment dans le détroit de Victoria et dans le détroit de Barrow (Figure 17). Ces deux dernières localités possèdent des régimes de courants qui sont possiblement à l'origine de la présence de ces communautés. De plus, plusieurs stations sur substrat rocheux ont été échantillonnées au cœur de l'archipel (détroit de Barrow, détroit de Franklin) et abritent de grandes biomasses et richesses benthiques qui ne pouvaient être adéquatement estimées avec l'usage du chalut scientifique Agassiz. D'autres techniques d'échantillonnage devront être envisagées pour bien étudier la diversité des communautés sur substrat rocheux et afin de limiter leur destruction, telles que l'usage de véhicules téléguidés (« *Remotely Operated Vehicle* ») ou de drones sous-marins (« *Autonomous Underwater Vehicle* »).

Les communautés benthiques de la macrofaune et mégafaune de l'Arctique canadien sont des intégrateurs à long terme de conditions environnementales variant à plusieurs échelles spatiales

De manière générale, la profondeur, les variables océanographiques à la base de la colonne d'eau (oxygène, température, salinité) et les indicateurs annuels et pluriannuels de la disponibilité des ressources alimentaires sont de bons facteurs explicatifs de la structure et distribution des communautés benthiques à la grandeur de l'Arctique canadien. Ces derniers facteurs environnementaux varient au-delà de l'échelle saisonnière et reflètent par conséquent des conditions environnementales intégratives, récurrentes et relativement stables. Il a été montré dans les chapitres 2, 3 et 4 que la variabilité spatiale des réponses des communautés benthiques étudiées domine par rapport à leur variabilité temporelle, du moins aux échelles étudiées, c'est-à-dire l'échelle régionale (mer de Beaufort-golfe d'Amundsen; chapitre 3) et continentale (Arctique canadien; chapitres 2 et 4) (Figure 35). Cette faible variabilité temporelle des communautés a permis dans le chapitre 3 d'assembler plusieurs bases de données sur près de 40 ans dans la mer de Beaufort et le golfe d'Amundsen entre 1973 et 2012 afin de créer des modèles prédictifs. La stabilité décennale, voire même plus, des patrons des communautés benthiques en Arctique a déjà été mentionnée lors d'études précédentes (Renaud *et al.* 2007c ; Carroll *et al.* 2008). Ce dernier aspect implique que les communautés benthiques sont des indicateurs à long terme des changements environnementaux et qu'afin de suivre ces changements il est primordial de maintenir des séries de données à long terme. Il est d'ailleurs dans ce sens recommandé dans le chapitre 3 que toute campagne d'échantillonnage future devrait veiller à bonifier les bases de données existantes en collectant au minimum le même type de données environnementales déjà recueillies.

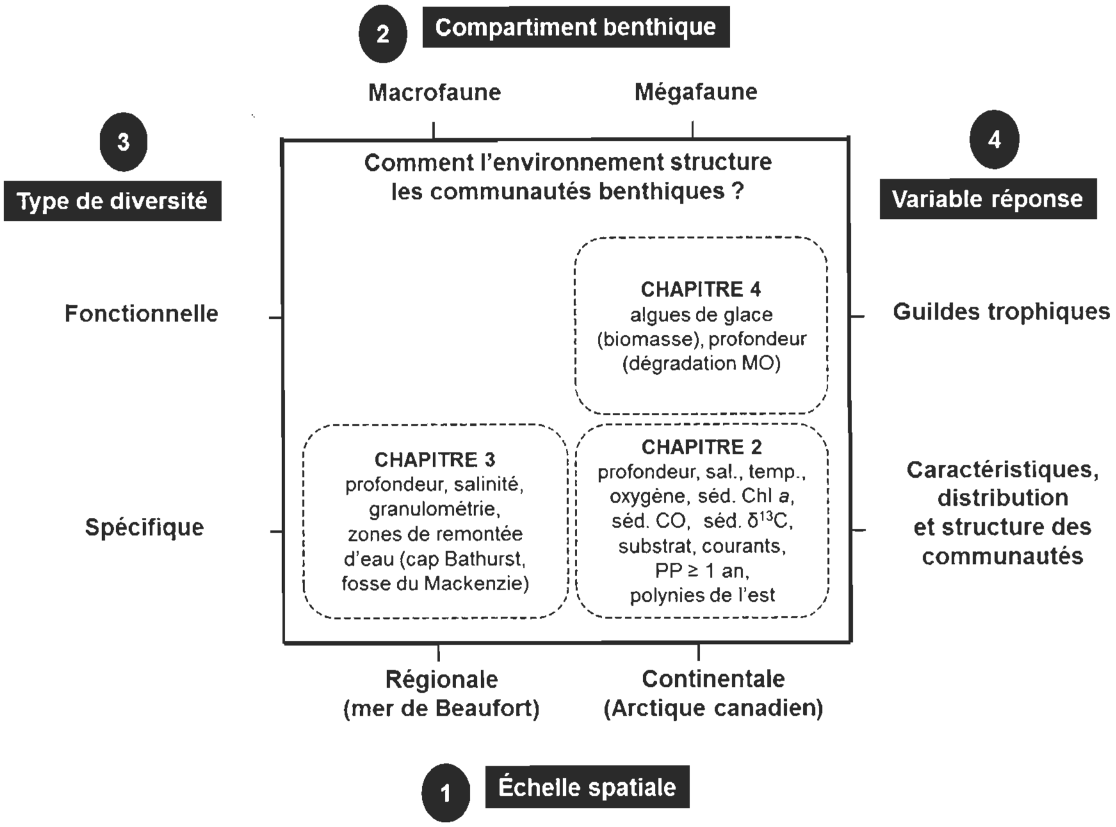

Figure 35. Synthèse des principales conclusions de cette thèse basée sur la question centrale de définir comment l'environnement structure les communautés benthiques de l'Arctique canadien. CO : carbone organique ; MO : matière organique ; séd : sédiment ; PP : production primaire.

Dans les chapitres 2 et 3, il a été montré que la variabilité spatiale des caractéristiques et de la distribution des communautés benthiques suivait le gradient vertical des variables océanographiques à la base de la colonne d'eau (ex. salinité), ces dernières caractérisant différentes masses d'eau (Pacifique et Atlantique). Les variables océanographiques sont parmi les facteurs environnementaux les plus accessibles à intégrer dans les études comme celles effectuées dans le cadre de cette thèse, car elles sont généralement disponibles à chaque station échantillonnée, et ce en peu de temps, ne requérant pas d'échantillonnage fastidieux et d'analyses en laboratoire. Cependant, alors qu'elles ressortent souvent comme des facteurs explicatifs des patrons des communautés benthiques à l'échelle régionale et continentale, aucune étude, incluant cette thèse, n'a pu déterminer si ces facteurs sont réellement d'importance directe pour les communautés benthiques. Ces facteurs sont en partie difficile à interpréter, car au large des zones côtières on les associe entre autres à des gradients biogéographiques et donc à l'histoire évolutive des espèces. Peu d'information existe sur ce sujet pour l'océan Arctique en général, et encore moins pour l'Arctique canadien. Les plateaux continentaux de l'océan Arctique sont peuplés de communautés benthiques « relativement jeunes » en termes d'évolution en raison des variations du niveau de la mer de l'ordre de 85-100 m entre les périodes glaciaires et interglaciaires (Dunton 1992 ; Piepenburg 2005). Pour l'Arctique canadien, il semble qu'à la fois les faunes marines du Pacifique Nord et de l'Atlantique Nord ont joué des rôles importants dans les phases de recolonisation des plateaux continentaux dans la période interglaciaire actuelle (Lubinsky 1972 ; Dunton 1992 ; Carr 2012). Dans le cas des zones profondes, la faune marine du Pacifique Nord n'a joué aucun rôle (Dunton 1992 ; Bluhm *et al.* 2011a). Il serait par conséquent utile de relier, davantage qu'il ne l'a été fait dans cette thèse, l'histoire géologique depuis la fin de la dernière glaciation avec les patrons actuels de distribution des communautés benthiques.

Il est démontré dans le chapitre 2 qu'il est difficile de généraliser les relations environnement – communautés benthiques à l'échelle continentale de l'Arctique canadien, car des conditions biologiques et physiques particulières sont présentes régionalement et/ou localement, et interfèrent par conséquent avec les tendances à grande échelle. Par exemple, la profondeur n'est pas un indicateur indirect fiable de la biomasse benthique dans l'est de l'Arctique canadien (détroit de Lancaster, polynie des eaux du Nord), car les communautés profondes de ces régions bénéficient d'un grand apport de ressources alimentaires en raison de la conjoncture d'une grande production primaire, d'une forte exportation de cette production hors de la zone euphotique et de forts courants qui possiblement aident à transporter cette production, même jusqu'à 800 m de profond à l'entrée du détroit de Lancaster. L'étude de Thomson (1982) avait déjà suggéré l'importance de courants profonds à l'entrée du détroit de Lancaster pour expliquer les fortes biomasses de benthos et la présence de taxa suspensivores. Par contre, la profondeur est un bon indicateur de la faible disponibilité de ressources alimentaires, et par conséquent de faibles densités, biomasses et richesses benthiques, dans les secteurs profonds de l'ouest de l'Arctique canadien (centre du golfe d'Amundsen, pente continentale de la mer de Beaufort), tel que vu dans le chapitre 3. Dans l'ouest de l'Arctique canadien, un ensemble de facteurs, dont une plus faible production primaire, une plus grande interception de cette production par les réseaux hétérotrophes pélagiques (Darnis *et al.* 2012) et possiblement de faibles courants, limite l'apport de ressources alimentaires aux communautés benthiques profondes et par conséquent, limite la biomasse, densité et richesse de ces communautés. Ces différences interrégionales révèlent qu'une plus grande disponibilité de données de flux verticaux de COP, à l'échelle de l'Arctique canadien et préférentiellement intégrées sur une année, permettrait de mieux comprendre l'influence indirecte de la profondeur sur les ressources alimentaires des communautés benthiques. Actuellement, les études principales portant sur des estimations annuelles de flux verticaux de COP se sont déroulées dans la mer de Beaufort (Forest *et al.* 2007), le golfe d'Amundsen (Forest *et al.* 2008 ; Forest *et al.* 2010) et la polynie des eaux du Nord (Hargrave *et al.* 2002).

Il a également été démontré dans le chapitre 2 que les indicateurs de la disponibilité des ressources alimentaires significativement retenues dans les analyses statistiques (Figure 35) n'expliquaient que modérément les patrons des caractéristiques et la distribution des communautés à l'échelle continentale de l'Arctique canadien. Ces résultats indiquent par conséquent qu'aucun des indicateurs de la disponibilité des ressources alimentaires testés ne permettait de résumer globalement la force du couplage pélago-benthique à l'échelle de l'Arctique canadien. Puisque il a été montré dans le chapitre 4 que les algues de glace sont certainement la source principale actuelle de carbone pour les réseaux trophiques benthiques de l'Arctique canadien, cela suggère qu'un indicateur de la biomasse d'algues de glace pour l'ensemble des stations à l'étude dans le chapitre 2, aurait vraisemblablement été bien corrélé avec la densité et la biomasse benthique. Toutefois, en raison de la multitude de facteurs environnementaux qui contrôlent la biomasse d'algues de glace (ex. épaisseur de glace, de neige, nutriments, lumière (Michel *et al.* 2006 ; Rozanska *et al.*

2009)), il s'est avéré impossible de trouver un indicateur global de cette production primaire.

En raison des résultats et conclusions du chapitre 2, il est fortement recommandé aux futures études benthiques effectuées à grande échelle (ex. échelle de l'Arctique canadien, voire même échelle panarctique), d'inclure une part de vigilance dans leurs prédictions ou du moins d'évaluer le niveau d'incertitude. Les études à grande échelle, comme celle du chapitre 2 sont essentielles pour explorer et définir les principaux gradients environnementaux d'influence, mais leur pouvoir prédictif ne peut être aussi grand que dans le cadre d'études régionales, telles que dans le chapitre 3, d'autant plus si les informations et modèles sont à l'intention d'instances gouvernementales afin d'être utilisés dans les processus stratégiques et décisionnels de conservation.

Première étude sur le lien entre la variabilité spatiale de la composition isotopique du carbone des invertébrés benthiques et la biomasse d'algues de glace dans l'Arctique canadien

Les résultats du chapitre 4 ont permis de montrer pour la première fois que les algues de glace seraient la source principale de carbone qui transite dans les réseaux trophiques benthiques, et ce à la grandeur de l'Arctique canadien. Ce fort couplage algues de glace – benthos était particulièrement évident dans les détroits de Barrow et d'Éclipse (Figure 27) où les signatures isotopiques en carbone indiquaient une assimilation d'algues de glace issues de fortes biomasses (Figure 31). Les études récentes montrant une relation positive entre la biomasse algale et la signature en $\delta^{13}C$ dans la glace (Tremblay *et al.* 2006b ; Gradinger 2009 ; Pineault *et al.* 2013) ont permis de comprendre le patron de variabilité spatiale de la signature en $\delta^{13}C$ des invertébrés benthiques exposé dans le chapitre 4. Des études antérieures présumaient déjà que les invertébrés benthiques échantillonnés dans les détroits de Barrow et Lancaster (Hobson & Welch 1992) et dans la polynie des eaux du Nord (Hobson *et al.* 2002) avaient des signatures en $\delta^{13}C$ élevées reflétant possiblement une assimilation de carbone en provenance des algues de glace. Toutefois, ces études n'avaient pas conclu clairement sur l'importance de cette production primaire pour les réseaux trophiques benthiques et le chapitre 4 apporte ainsi une importante contribution scientifique à notre compréhension du couplage pélago-benthique à l'échelle de l'Arctique canadien. Il semble ainsi que le paradigme avancé par plusieurs auteurs d'un fort couplage algues de glace – benthos dans d'autres régions arctiques (Carroll & Carroll 2003 ; Piepenburg 2005 ; Bluhm & Gradinger 2008) s'applique également à l'Arctique canadien. La récente étude de Søreide *et al.* (2013) montre également, par l'étude des isotopes stables du carbone, que les communautés benthiques de l'archipel de Svalbard assimilent principalement du carbone issu des algues de glace. Bien que le chapitre 4 apporte de nouvelles données, les portées des conclusions sont limitées et beaucoup d'aspects restent à être élucidés. La principale limite de cette étude est que les algues de glace n'ont pu être échantillonnées au même moment que la collecte des invertébrés benthiques. Par conséquent, les valeurs de la littérature de zones échantillonnées qui chevauchaient les stations de cette étude ont été utilisées. Logistiquement, que ce soit à partir de camps de glace ou à partir de navires de recherche, il est très difficile de pouvoir échantillonner les algues de glace en même temps que le benthos durant la période de sédimentation des algues qui coïncide avec la fonte de la glace. Toutefois, puisque les signatures isotopiques dans les tissus musculaires des invertébrés étaient stables sur au moins deux mois, il reste qu'il n'est peut-être pas essentiel d'avoir accès aux algues de glace au moment précis de l'échantillonnage des invertébrés benthiques, mais il faut minimalement un chevauchement spatial des données d'algues de glace et de benthos.

Première étude sur l'influence du gradient de profondeur sur la dégradation des ressources alimentaires assimilées par les invertébrés benthiques de l'Arctique canadien

Le fort impact du gradient de profondeur sur les compositions isotopiques en azote du réseau benthique dans le chapitre 4 peut paraître en opposition avec les faibles relations négatives établies entre la profondeur et les caractéristiques des communautés (ex. biomasse, richesse) du chapitre 2. Les conclusions de ces deux chapitres ne se contredisent pas cependant, car la signature isotopique en azote ne permet pas d'inférer sur la quantité totale de ressources alimentaires reçue par les communautés benthiques, mais bien sur le degré de dégradation. Ainsi, des communautés benthiques profondes peuvent recevoir des ressources alimentaires en quantité, ce qui se traduira par de fortes biomasses benthiques, mais ces ressources alimentaires auront transité néanmoins par les réseaux hétérotrophes pélagiques avant d'atteindre le fond, tel que l'illustre la variabilité de la signature isotopique en azote. Les résultats combinés des chapitres 2 et 4 apportent ainsi une interprétation globale plus juste et nuancée sur l'impact indirect de la profondeur sur la quantité et la qualité des ressources alimentaires disponibles aux communautés benthiques profondes.

Le chapitre 4 a permis également de montrer pour la première fois dans l'Arctique canadien que le groupe trophique des prédateurs-charognards des communautés benthiques profondes ($\geq$ 200 m) était possiblement limité par le nombre de proies et/ou de carcasses par rapport à leurs homologues sur le plateau continental (< 200 m). Ce résultat démontre une augmentation du comportement omnivore avec la profondeur et a donc une portée scientifique notable dans notre compréhension du mode alimentaire des invertébrés benthiques. La majorité des études ont établi les modes alimentaires des invertébrés en zones peu profondes et l'on reprend ces informations en supposant que le même organisme dans un milieu profond conservera un comportement alimentaire similaire, ce qui peut se révéler faux, comme cela est souligné dans le chapitre 4. De plus, il n'existe pas d'expériences d'alimentation (« *feeding experiment* ») pour la majorité des espèces présentes dans l'océan Arctique, et par conséquent on attribue souvent le mode alimentaire d'une espèce en se basant sur les informations disponibles au niveau du genre, ou même de la famille. Par conséquent, étudier la variation du niveau trophique (au moyen de la composition isotopique en azote) le long de gradients environnementaux, tels que la profondeur est, selon moi, une approche prometteuse pour mieux élucider les comportements alimentaires des organismes benthiques et enrichir la modeste littérature scientifique existante sur ce sujet.

Implication pour le suivi à long terme des communautés benthiques en fonction des changements climatiques en cours et prédits

Les données de référence ainsi qu'une meilleure compréhension du contrôle environnemental sur les communautés benthiques qu'apporte cette thèse permettront d'entreprendre un suivi des impacts potentiels des changements climatiques. Certains sites ou régions devraient être rigoureusement suivis sur une assez longue période de temps afin de s'assurer que les changements mesurés soient bien directionnels et non liés à la variabilité stochastique de l'écosystème (Glover *et al.* 2010). En regard des changements climatiques en cours et prévus, voici les régions sentinelles que je propose de suivre plus spécifiquement et les raisons associées :

Plateau continental du Mackenzie

Il a été démontré dans les chapitres 1 et 2 que la composition taxonomique des communautés de la mégafaune est très distincte dans cette région comparativement au reste de l'Arctique canadien en raison de l'influence de la rivière Mackenzie. L'influence terrestre sur les écosystèmes marins arctiques devrait augmenter selon les prédictions d'augmentation des précipitations, du débit des rivières et de l'érosion côtière (Carmack & McLaughlin 2001; Piepenburg 2005; Walsh 2008). De plus, la réduction du couvert de glace conduira certainement à une emprise accrue du vent et donc à l'augmentation des tempêtes, des vagues et des inondations côtières (Walsh 2008). Tous ces changements pourraient entraîner des perturbations physiques directes sur les habitats benthiques (ex. érosion et apport sédimentaire accru). Les changements environnementaux pourraient également modifier la disponibilité des ressources alimentaires pour le benthos selon les impacts que ces changements auront sur la production primaire et son exportation vers le fond marin. D'ailleurs, la production primaire par les algues diatomées dans le domaine côtier de la mer de Beaufort a augmenté dans la dernière décennie (Bergeron & Tremblay 2014). Les modèles de distribution de la richesse, densité et des communautés benthiques de la macrofaune du chapitre 3 constituent donc un excellent cadre de référence pour suivre les impacts potentiels de ces changements climatiques et de la production primaire dans l'avenir.

Polynies du détroit de Lancaster et des eaux du Nord

L'influence positive qu'ont ces deux polynies sur les fortes richesses et biomasses des communautés benthiques profondes situées en dessous a été démontrée dans le chapitre 2. Toutefois, plusieurs changements environnementaux en cours et à venir pourraient perturber le fort couplage pélago-benthique présent dans ces polynies, reconnues comme étant parmi les plus productives de l'océan Arctique (Tremblay & Smith Jr. 2007). D'une part, l'analyse de la variation temporelle d'estimations de production primaire obtenues par satellite sur la période 1998-2010 a montré une tendance à la baisse dans ces deux polynies (Bélanger *et al.* 2013). Des mesures *in situ* ont d'ailleurs confirmé une baisse de la production primaire par les algues diatomées dans la polynie des eaux du Nord (Bergeron & Tremblay 2014). D'autre part, la tendance continue du réchauffement de la température de surface de l'océan Arctique est prévue favoriser la croissance de cellules plus petites de phytoplancton (ex. picophytoplancton) au détriment des grosses cellules (ex. diatomées) (Li *et al.* 2009). Puisque qu'il est connu que les grosses cellules phytoplanctoniques sédimentent rapidement et contribuent donc en majeure partie au flux de carbone atteignant les fonds marins (Wassmann 1998), une transition vers des communautés phytoplanctoniques constituées de petites cellules entraînera fort possiblement une diminution du fort couplage pélago-benthique qui existe actuellement dans ces deux régions profondes où de fortes biomasses benthiques sont observées.

PERSPECTIVES

Définir l'importance du couplage physique-biologie pour le transport et l'approvisionnement en ressources alimentaires des communautés benthiques

Les résultats du chapitre 2 suggèrent que de riches communautés mégabenthiques, en terme de biomasse, sont susceptibles d'être découvertes dans l'archipel canadien, parce qu'y sont présents de forts régimes de courants. Si les courants ont un effet positif sur la densité et la biomasse benthique, c'est qu'indirectement ils transportent ou remettent en suspension de grandes quantités de ressources alimentaires (Snelgrove & Butman 1994). Ces régimes de courants peuvent exister sous plusieurs formes, que ce soit en raison des mouvements de marée en eaux peu profondes, d'une resuspension de sédiment, à cause d'une combinaison d'une topographie abrupte (ex. pente) et d'une remontée d'eau ou par la présence d'un courant de fond en eaux profondes. Des études intégratives portant sur les régimes de courants et la circulation de l'eau et leur influence sur les productions primaires sympagique et pélagique (ex. par l'apport de nutriments) et leur sédimentation subséquente hors de la zone euphotique sont inexistantes à ma connaissance pour l'archipel canadien. Il est par conséquent difficile à ce jour de bien comprendre le couplage de conditions physiques et biologiques qui semble très important au cœur de l'archipel. Il serait par conséquent fort intéressant de comprendre davantage ce couplage physique-biologie afin de prévoir comment les changements climatiques pourront nuire ou avantager les conditions actuelles favorables au benthos. Entre autres, l'étude de Hannah *et al.* (2009) a cartographié pour l'archipel différentes caractéristiques des courants de marée (force, mélange et excursion verticale d'eau). Les points chauds que les auteurs ont établis pourraient servir de « cibles benthiques » dans un processus exploratoire de nouvelles zones à échantillonner. Dans les zones plus profondes, où les courants de marée ont un impact réduit, les zones de forts courants de fond et de fortes pentes pourraient être cartographiées afin de cibler des localités où il est envisageable de trouver de fortes biomasses benthiques en raison de l'action positive des courants sur le transport et l'approvisionnement en ressources alimentaires.

Approfondir l'importance des algues de glace comme source majeure de carbone pour les réseaux trophiques benthiques de l'Arctique canadien

Dans plusieurs études récentes (Søreide *et al.* 2013 ; Carroll *et al.* 2014), incluant celle du chapitre 4, la composition des isotopes stables du carbone mesurée sur les tissus musculaires ou le matériel entier (« *bulk material* ») a montré une variabilité temporelle assez stable chez les invertébrés benthiques arctiques, ce qui en fait un outil biochimique d'excellence pour étudier la variabilité spatiale de la diète du benthos, mais il ne permet pas d'infirmer avec certitude que le benthos a assimilé des algues de glace. Le marqueur lipidique IP_{25}, spécifique aux algues de glace, pourrait être ainsi utilisé comme un outil complémentaire aux isotopes stables, car la présence de ce marqueur dans les tissus des invertébrés benthiques soulignerait précisément que ces derniers ont assimilé du matériel organique dérivé des algues de glace (Brown & Belt 2012). Il serait intéressant également de déterminer la variabilité saisonnière de la diète des organismes benthiques. Un outil biochimique de choix pour un tel objectif serait les acides gras (Søreide *et al.* 2013). D'une part, les profils d'acides gras des invertébrés benthiques permettraient de distinguer la composition relative de leur diète, par exemple en termes de diatomées, dinoflagellés et de bactéries (Søreide *et al.* 2013 ; Wang *et al.* 2014). Ceci permettrait entre autres d'affirmer ou de réfuter l'hypothèse avancée par certaines études récentes que les valeurs élevées en $\delta^{13}C$ rapportées pour les invertébrés benthiques de l'Arctique pourraient provenir d'une assimilation importante de bactéries et/ou de matériel organique ayant transité par le réseau microbien benthique (Lovvorn *et al.* 2005 ; McTigue & Dunton 2013). Des études récentes permettent en partie de réfuter déjà ce postulat, car elles ont montré une faible proportion d'acides gras en provenance des bactéries (Søreide *et al.* 2013 ; Wang *et al.* 2014), mais cela n'a pas été démontré pour l'Arctique canadien. D'autre part, la détermination de la composition des isotopes stables du carbone sur les acides gras individuels permettrait de distinguer plus précisément l'origine d'un élément de la diète, par exemple en déterminant si ce sont des diatomées de glace ou diatomées pélagiques qui ont été assimilées (Wang *et al.* 2014). Point intéressant, à la fois le $\delta^{13}C$ du COP dans la glace (tel que vu dans le chapitre 4 ; Pineault *et al.* 2013) et le $\delta^{13}C$ des acides gras spécfiques du COP dans la glace

(Wang *et al.* 2014) tendent à augmenter avec une augmentation de la photosynthèse, en raison d'une baisse de la discrimination envers le ^{13}C lorsque les réserves de carbone inorganique dissous baissent dans les canaux internes de la glace.

Alors que la diminution du couvert de glace laisse présager une diminution de l'importance du flux de carbone en provenance des algues de glace vers le benthos (Bluhm & Gradinger 2008), le couplage algues de glace – benthos pourrait en fait augmenter dans certaines zones de l'archipel arctique canadien où il y a actuellement de la glace multiannuelle (ex. Haut-Arctique). La production d'algues de glace peut être limitée en raison de plusieurs facteurs environnementaux, dont l'épaisseur de la glace et la couverture de neige qui atténuent la lumière (Michel *et al.* 2006 ; Rozanska *et al.* 2009). Ainsi, les déclins continus observés de l'épaisseur de la glace de mer (Sou & Flato 2009) et de l'épaisseur de la neige (Serreze *et al.* 2000) pourraient favoriser une production accrue d'algues de glace dans ces régions dans un proche avenir, bien que les prévisions à long terme prévoient globalement pour l'océan Arctique une diminution de l'apport d'algues de glace vers le benthos. L'analyse des valeurs isotopiques en carbone des invertébrés benthiques dans ces zones pourrait permettre de définir l'importance des algues de glace dans leur diète. De plus, un suivi à long terme de l'évolution de leurs diètes suivant une diminution de la couverture de glace multiannuelle pourrait être entreprise.

Recenser les expansions latitudinales des espèces boréales

Aucune espèce benthique non indigène à l'Arctique canadien n'a été découverte dans les chapitres de cette thèse. Cependant, l'intensification des changements environnementaux et des activités humaines pourrait favoriser l'introduction intentionnelle ou non de telles espèces dans l'avenir. Par exemple, il y a le cas de l'introduction intentionnelle du crabe royal du Kamtchatka (*Paralithodes camtschaticus*) dans la mer de Barents (Jørgensen 2005). Le réchauffement et l'expansion de la couche d'eau profonde d'origine atlantique dans l'océan Arctique (Serreze *et al.* 2000) pourraient favoriser l'expansion latitudinale des espèces boréales de l'Atlantique Nord dans l'océan Arctique. Parallèlement, une augmentation de l'entrée de la couche d'eau de surface en provenance du Pacifique Nord (« *buoyancy boundary flow* ») (Carmack & McLaughlin 2001) pourrait entraîner une augmentation des importations d'espèces boréales d'origine pacifique. Les changements dans les propriétés physiques des masses d'eau et les courants peuvent en effet favoriser l'expansion latitudinale de certaines espèces, comme cela est observé pour le crabe des neiges (*Chionoecetes opilio*) dans la mer de Chukchi (Bluhm *et al.* 2009) et la moule bleue (*Mytilus edulis/trossulus*) dans la mer de Barents (Wassmann *et al.* 2006). L'augmentation du trafic maritime pourrait également favoriser l'introduction d'espèces envahissantes (Molnar *et al.* 2008). L'expansion des aires de distribution des espèces benthiques boréales et les introductions potentielles de nouvelles espèces changeront d'une part la composition spécifique actuelle des communautés benthiques et d'autre part entraîneront possiblement des interactions concurrentielles néfastes au sein des communautés (ex. compétition sur les ressources alimentaires). Les bases de données taxonomiques que lègue cette thèse sont ainsi un excellent cadre de référence pour suivre cette problématique émergente en Arctique.

Autre facteur environnemental d'importance : l'hétérogénéité topographique du milieu benthique

Les études réalisées en Arctique, incluant cette thèse, font généralement référence à l'hétérogénéité du sédiment en testant la variabilité du substrat (dur ou meuble) ou de la taille des grains du substrat (granulométrie), et non pas en testant la variabilité du terrain ou de la topographie sur les caractéristiques des communautés benthiques. Il est reconnu par ailleurs que la variabilité de la topographie a un effet positif sur la diversité spécifique en augmentant le nombre de niches disponibles, tant en milieu terrestre (Luoto *et al.* 2004 ; Parks & Mulligan 2010 ; Yamaura *et al.* 2011) qu'en milieu marin (Archambault & Bourget 1996 ; Desrosiers *et al.* 2000 ; Kostylev *et al.* 2005 ; Lundblad *et al.* 2006 ; Dunn & Halpin 2009 ; McArthur *et al.* 2010 ; Brown *et al.* 2011).

La caractérisation à fine échelle de la topographie des fonds marins en zones profondes se fait aujourd'hui entre autres au moyen de sonars multifaisceaux (« *multibeam* ») qui procurent une haute densité de données de bathymétrie servant à générer des variables quantitatives descriptives du terrain (Wilson *et al.* 2007 ; Buhl-Mortensen *et al.* 2009 ; Buhl-Mortensen *et al.* 2012). L'article de Wilson *et al.* (2007) discute de quatre grandes classes de variables de terrain qui peuvent être dérivées de ces données bathymétriques, soit la pente, l'orientation (l'aspect), l'indice relatif bathymétrique et la variabilité du terrain (c.-à-d. la complexité ou la rugosité du terrain). Il faut considérer qu'en plus du choix des variables de terrain d'intérêt, à la fois la résolution des données bathymétriques et l'échelle de la fenêtre d'analyse influencent le pouvoir explicatif de telles mesures de terrain en écologie benthique. Par exemple, la majorité des études reliant la topographie aux communautés benthiques sont accomplies dans les environnements moyennement profonds (< 250 m) avec une résolution fine de la bathymétrie (cm au m) et sur une aire d'étude inférieure à 10 km^2 (Brown *et al.* 2011). Les résultats sont donc peu applicables à d'autres échelles et à d'autres milieux. Dans le cas de l'Arctique canadien, j'ai constaté que la résolution, la qualité et la couverture spatiale des données multifaisceaux disponibles à ce jour ne permettaient pas de calculer des variables de terrain (ex. rugosité) ayant une valeur écologique pertinente en regard du phénomène étudié. En effet, les données multifaisceaux actuelles contiennent trop de bruits et d'artefacts (ex. dû aux bulles sous la coque du brise-glace et/ou dû aux données elles-mêmes). De plus, la majorité des stations de cette thèse étaient sur substrat meuble où un lissage des données enlevait toute rugosité perceptible à partir d'une résolution de 10 m (résolution des données multifaisceaux de l'*Amundsen*. À court terme, des études pourraient porter sur l'hétérogénéité de l'habitat à de grandes échelles spatiales, en utilisant par exemple la base de données IBCAO ayant une résolution de 500 m (« *International Bathymetric Chart of the Arctic Ocean* »). Néanmoins, l'usage des variables de terrain à une fine échelle spatiale est prometteur pour des études futures dans l'Arctique canadien et je recommande que ces études se concentrent à l'échelle régionale (et non continentale), en zones peu profondes (< 200 m) pour garantir un maximum de couverture de données et de résolution (2 m à 5 m, contre 10 m à > 200 m) et en zone de substrat rocheux pour garantir une variabilité du terrain suffisamment mesurable et écologiquement pertinente. Actuellement, le plateau du

Mackenzie dans la mer de Beaufort est la principale région qui remplit au mieux les deux premiers critères, mais cette région est majoritairement sur substrat meuble.

CONCLUSION

Les données de référence qu'apporte cette thèse, ainsi qu'une meilleure compréhension de la complexité des relations environnement – communautés sur plusieurs échelles spatiales, constituent une base scientifique importante pour de futures recherches ayant comme objectif l'approfondissement des processus et des mécanismes à l'origine des relations identifiées. Dans ce sens, l'importance d'étudier davantage le rôle des régimes de courants pour expliquer la présence de points chauds (« *hotspots* ») de biomasses benthiques dans des zones profondes et oligotrophes où l'on aurait pu prédire à tort de faibles biomasses a été soulevée. Cette thèse a mis l'emphase sur la nécessité de définir les échelles de variabilité spatiale et temporelle des facteurs environnementaux à l'étude afin de mieux interpréter comment ils structurent les communautés benthiques. Malgré que cette approche améliore notre conception du contrôle environnemental sur les communautés benthiques, plusieurs pistes de réflexion restent ouvertes pour élucider complètement les processus écologiques et évolutifs qui ont mené à la représentation spatiale actuelle des communautés benthiques que nous observons. L'Arctique canadien est un environnement en changement et les bases de données d'espèces et de données environnementales qui ont été générées par l'entremise de cette thèse permettront, entre autres, d'entreprendre un suivi des impacts des changements climatiques et anthropiques à venir sur la diversité et la distribution des communautés benthiques. Enfin, les résultats de cette thèse ont servi et pourront encore servir dans les processus canadiens de désignation des zones d'importance écologique et biologique (ZIEB), une étape importante en vue d'adopter une approche plus globale de gestion de l'environnement maritime arctique et afin d'orienter des initiatives régionales de planification d'aires marines protégées.

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